CONTROL OF GROWTH REGULATORS AND TEMPERATURE ON SEEDSTALK DEVELOPMENT, SEED YIELD AND SEED QUALITY IN CARROTS (*Daucus carota* L.)

BY

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To my Mom and Dad,
Huda and Ala

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Abstract of Thesis Presented to the Graduate School
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Harvested carrot seeds vary greatly in their maturity due to the variation in umbel order formation on the mother plant. The effects of chemical regulators on seedstalk development, seed yield and seed quality in carrots were studied in greenhouse experiments. Ancymidol at 25 to 250 ppm, Daminozide at 1000 to 5000 ppm and hand pruning of the tertiary umbels reduced the number of branches per plant and the amount of seed produced by the tertiary and quaternary umbels. Total seed yield was reduced by Ancymidol and hand pruning. Application of GA_3 at 1000 ppm, Chlormequat at 2000 or 5000 ppm or Phosphon-D at 250 or 500 ppm, had no effect on number of branches or seed yield. Seed quality was not improved by Ancymidol, Daminozide or hand pruning, despite the reduction in the number of branches. That seed quality was not improved by either chemical or hand pruning was attributed to the reduction of seed yield from tertiary umbels, which had the highest quality and produced the largest seedlings compared to primary and secondary umbel seeds, regardless of treatment. Delaying the harvest of carrot seeds under field conditions until the tertiary umbel seeds reach full maturity is recommended to improve overall seed quality and yield.

Temperature during seed formation was varied to determine its effects on seed quality. The number of days to flowering, seedstalk height, number of umbels and seed yield decreased linearly with the increase in temperature from 17/12°C to 33/28°C (day/night). Seeds which matured at 20/15°C and 25/20°C had the highest total germination and germination rate, compared to those matured at 33/28°C, 28/23°C, 23/18°C or 17/12°C. A brief exposure (10 days) of the carrot plants to 33/28°C at anthesis or in early seed development was as detrimental to seed yield and quality as continuous high temperature (i.e., 33/28°C), while exposure to high temperature at late seed development had less effect on seed yield and improved seed quality.

The possibility of improving the performance of commercial seedlots by incorporating growth regulators during priming was investigated. Soaking carrot seeds in -10 bar PEG for 7 or 14 days at 15°C was the best priming treatment in improving seed performance. Seeds of three seedlots tested failed to germinate at 35°C before priming. Seed priming in PEG improved seed germination at 35°C regardless of seedlot. Addition of growth regulators (i.e., BA, GA_3, $GA_{4/7}$ or Ethrel) to PEG did not give any additional benefit compared to priming in PEG alone.

CHAPTER ONE
INTRODUCTION

Carrot (Daucus carrota L.) is an important vegetable crop in Florida. There were 11,500 acres harvested from the 12,500 acres planted during the 1984-1985 crop years. Total cash value for 1984-1985 crops was $11.4 million. Approximately 95% of harvested carrots in Florida were grown in the muck soils around Lake Apopka, near Zellwood. The remainder were produced on the muck soil of the Everglades (Florida Agricultural Statistics, 1985). Nationally, Florida ranks third in fresh market carrot production, after California and Texas.

Uniform field stands are a major limiting factor in the production of carrot. Seed quality is considered a major factor contributing to poor field stands. The lowest standards of germination in horticultural seeds are in the Umbelliferous seed crops. The germination standards according to the Federal Seed Act are 55% for carrot, celery and celeriac, and 60% for parsley and parsnip (Robinson, 1954).

In spite of more than two decades of research on improving carrot seed quality, a considerable proportion of carrot seed lots produced each year have low germination percentages (less than 70%). This results in poor field emergence especially under adverse field conditions, like the high and low temperatures prevailing in Florida between August and September and December and February, respectively.

The results of previous research have shown that poor seed quality in carrot might be caused by one or a combination of the following factors:

1) Flowering morphology of the seed plant,
2) Environmental conditions during seed development,
3) Level of pollination,
4) Seed crop diseases and pest damages, and
5) Cultural practices--plant density and harvest time.

Most of the research on carrot seeds since 1978 has dealt with the effects of plant morphology on seed vigor. A strong connection between seed vigor and the position of seed on the parent plant was established by many workers (Gray, 1983). In view of these results it is tempting to investigate the possibility of modifying plant morphology and study the effects of such methods on seed yield and vigor. So far, practical and economically feasible methods for such modification is unavailable.

The environment during seed development dictates the location of seed production for many crops. Temperature is a primary factor that influences the seed crop from its vegetative phase through seed development and maturation. Few reports on the temperature response in carrot have dealt mainly with the early stages of the seed plant growth. Such reports short of evaluating temperature effects on seed yield, seed quality and seedling growth.

Priming of seed in an osmoticum has been reported to increase field stands, advance emergence and increase germination percentage (Heydecker, 1975). Inclusion of growth regulators in such treatments might improve the efficacy of the treatment.

In an effort to improve seed quality and thereby plant stands of carrots, the main objectives of the present investigation were

1) To define the effect of seed stalk development on seed yield and seed quality in carrots through the use of growth regulators,

2) To study the effects of temperature on seed stalk, flowering, umbel formation, seed set and seed vigor, and

3) To study the effects of growth regulators inclusion in priming solution on the germination of different carrot seed lots.

CHAPTER TWO
LITERATURE REVIEW

Factors Affecting Seed Yield and Germination in Carrot and Other Umbelliferae Crops

Flowering Behavior and Harvest Date

The flowering behavior of carrot, which is typical to most Umbelliferae was described by many investigators (Borthwick, 1931a; Hawthorn and Pollard, 1954; Hawthorn et al., 1960; Gray and Steckel, 1977, 1980). Carrot flowers are produced in compound umbel borne terminally on the branches. The main axis in a carrot plant form the first order or primary umbel. From this main axis, several lateral branches arise producing secondary umbels. Lateral branches from the main stems bearing the secondary umbels form tertiary umbels and so on. Usually, however, only a few quaternary umbels are formed (Borthwick, 1931a; Gray and Steckel, 1980). Because of this habit of growth, anthesis and fertilization in any one plant proceed by waves, each wave corresponds to one umbel order. The interval between fertilization (petal fall) is about 10 days between primary and secondary umbels, but up to 20 days between the secondary and tertiary umbels (Borthwick, 1931a).

Carrot pollen dehiscence lasts 1 to 2 days and the stigma becomes receptive on the 3rd or 4th day and probably a week from style separation (Borthwick, 1931b). These floral events are more applicable and true with the open-pollinated cultivars. In the F_1 hybrid seed production, Dickson and Peterson (1978) reported that many parent lines show a considerable asynchromy of pollen dehiscence and stigma receptivity, which account for the poor seed yield in carrot hybrids. Flowering time and duration vary considerably between plants within a cultivar, cultivars and seed fields (Hawthorn, 1951a).

The complexity of the inflorescence structure in Umbelliferae results in production of seed on different positions on the mother plant. It was reported that seed position on the parent plants influenced seed size and quality in many plant species: barley (Austin, 1979), wheat (Rawson and Evan, 1970; Bremner, 1972), _Rumex crispus_ (Maur and Cavers, 1971), lettuce (Soffer and Smith, 1974), oilseed rape (Mendham and Scott, 1975), carrots (Borthwick, 1931a; Gray and Steckel, 1980; Jacobsohn and Globerson, 1980), and celery (Thomas _et al_., 1979).

In carrots, the growth of the seed is progressively delayed the lower the umbel order (Gray and Steckel, 1980). At maturity, the primary umbels have the largest seeds (Shevtsova and Khleborodov, 1975; Malik and Kanwar, 1969; Gray and Steckel, 1980; Jacobsohn and Globerson, 1980) and the tertiary umbels the smallest (Jacobsohn and Globerson, 1980).

Borthwick (1931a), Austin and Longden (1967), Castra and Andrews (1971), Jacobsohn and Globerson (1980), Hawthorn _et al_. (1962) and Malik and Kanwar (1969) reported that carrot seed germination is positively correlated to seed size. They indicated that larger seeds germinate and emerge better than small seeds; however, Gray and

Steckel (1983) reported that seed grading alone is an ineffective method of eliminating what they called seedborne sources of variation in seedling weight associated with umbel orders.

The effects of flowering habit on seed germination and subsequent seedling growth have been reported for carrots (Borthwick, 1931a; Hawthorn _et al_., 1962; Gray, 1979; Gray and Steckel, 1980, 1983; Shevtsova and Karol, 1977; Krarup and Villanueva, 19771a, 1977b). These effects are to be expected from the considerable differences in the time of flowering of different umbel orders. Borthwick (1931a) reported that carrot seeds from the primary umbels gave a germination of 81%, slightly better than the seeds from the secondaries, which gave 78%, and these in turn germinated better than the seeds from the tertiaries which gave 69% germination. Similar results have been reported by Hawthorn _et al_. (1962) and Nath and Kalvi (1969). Jacobsohn and Globerson (1980) compared seeds of the same size from different umbel order. They showed that seeds from the primary umbels gave higher germination than those of the same size from secondary and tertiary umbels.

Shevtsova and Koral (1977) and Krarup and Villanueva (1977a) have shown that carrot seeds from primary umbels gave larger plants and higher yielding crops than seed from higher umbel orders. However, Gray and Steckel (1980) showed that seeds from secondary umbels gave larger plants than seed of the same size from primary umbels. This might be an indication to the confounding of umbel effects with seed size or an interaction of the environment with umbel effect and harvest time.

The variation in embryo size within seeds in the population could be a source of variation in carrot roots (Glendhill, 1970). This was confirmed by Gray and Steckel (1980, 1983) and Gray et al. (1986) who reported that seedlings from seeds of primary umbels had smaller coefficient of variation (CV) values of seedling weight than those from secondary umbels, and this correlated well with the variability in embryo size. Both the CV of seedling weight and the CV of root weight in 16 lots of carrot increased with an increase in the CV of embryo length (Gray et al., 1986).

Krarup and Villanueva (1977a), in their series of investigation on carrot seed germination, found that the length of embryos from primary umbels was slightly greater than that from secondary umbels, but both samples germinated equally well. Embryo length and seed germination from tertiary umbels were significantly less. Grusvichiji et al. (1963) found considerable variability in embryo length. In mature carrot seeds, the length of embryos ranged from 0.3 to 2.0 mm. Differences in embryo length were found to result from seed size, umbel order, cultivar, the area and season of seed production.

In celery seed, which has a light requirement for germination, Nettles and Poe (1974) have shown that the percentage and rate of germination was greater from seed from the primary umbels, than from the lower umbel orders. Percentage germination also increased progressively with increased seed density, and as the largest and heaviest seeds were from the primary umbels, it could be concluded that germination was also highest from these.

Their results, however, were contradicted by the work of Thomas _et al_. (1979), using the celery cultivars Lanthorn Blanching, Ely White and Green Snap. Although they confirmed that the primary umbels produced the heaviest seeds followed by the secondaries, tertiaries and quaternaries, germination in the light at 18°C was lowest in the primaries, as a result of immature and shrivelled embryos, and highest in the tertiaries and quaternaries. The upper temperature limit was higher in the primaries and secondaries than in the tertiaries and quaternaries, suggesting positional effects on the level of dormancy. This suggestion is supported by the response of seeds to exogenous growth regulators. In all three cultivars, $GA_{4/7}$ stimulated germination in the dark, but the response was lower for the quaternary than primary umbels. All viable seeds from all umbels germinated equally well in a mixture of $GA_{4/7}$ plus BA, suggesting that the seeds arising from the later-formed umbels are deficient in cytokinins and perhaps other hormones necessary for breaking the dormancy, or might contain higher concentrations of germination inhibitors than those formed first, since it has been demonstrated that celery seed dormancy is being controlled by an interaction between promoters and inhibitors (Thomas _et al_., 1975).

A major proportion of the seed in commercial carrot crops comes from the secondary umbels, which have a lower germination than seed from the primary umbels (Borthwick, 1931a; Hawthorn _et al_., 1962; Castra and Andrew, 1971; Krarup _et al_., 1976; Gray and Steckel, 1980). The primary umbels' contribution ranged between 5 and 15% of seed yield. Secondaries ranged between 41 and 53%, while the tertiaries contributed about 36 to 50% (Borthwick, 1931a; Hawthorn et al., 1962; Krarup and Villanueva, 1977a).

Using Borthwick's 1931 yield and germination data, Gray and Thomas (1982) estimated that mean germination of the crop of seeds from all umbels would be 72% compared with 81, 78, 69, and 51%, respectively, for the primaries, secondaries, tertiaries, and quaternaries separately. The germination of the seedlot of which 90% was from the secondaries was only marginally affected by the presence in the seedlot of seeds from lower umbel orders. Mixing seeds from different umbel orders together in proportions which stimulate their contribution to the yield of seed from the whole plant, increased the CV of seedling weight compared with that obtained by examining seeds from separate umbel orders (Gray and Steckel, 1980).

Jacobsohn and Globerson (1980) and Gray (1981) suggested that since better quality seed is produced from the primaries than from lower umbel orders, efforts should be made to grow crops in such a way as to reduce the proportion of yield contributed by the lower orders. Early workers (Hagije, 1954; Miyagi, 1956; Krarup et al., 1976) have shown that removing the secondary umbels of carrot during early plant growth increased seed size and improved seed viability. But they did not report the effects on subsequent seedling and root variability. Even if this technique was to reduce variability, it would probably be economically infeasible, as seed yields are greatly reduced and the intensive labor nature of the operation is prohibitive (Gray, 1983).

Seed Maturity

In order for a fertilized ovule to develop into a fully mature seed, many essential processes are involved and certain factors play important roles in these processes. Typically, three stages can be distinguished in the development of the seed after pollination: development of the embryo, accumulation of food reserves, and the ripening or desiccation of the seed (Thompson, 1979).

After sexual fusion, the growth of the embryo in carrot is slow at first, while that of the endosperm is rapid. At the early stage of development, the central cavity within the immature seed is nearly filled with endosperm tissue, while the embryo still contains a few cells. Later in the development, part of the endosperm is digested as the embryo elongates and pushes into the central part of the seed (Borthwick, 1931b). In a recent study, Gray *et al*. (1984) reported that maximum carrot seed dry weight and maximum endosperm volume were reached about 35 days after anthesis. At this time the endosperm was still soft, and less than 50% of the seeds were viable. Fully ripe seeds were not produced until 44 days later. Both Borthwick (1931b) and Gray *et al*. (1984) showed that most of the increase in carrot seed endosperm volume was due to an increase in cell number, which ceased 35 days after anthesis. The increase in embryo volume was slower and was due to an increase in both cell number and cell volume which continued until 49 days after anthesis. At maturity the embryo was the equivalent of between 2 and 3% of the endosperm volume (Gray *et al*., 1984).

The determination of seed maturity is more complicated in the Umbelliferae by the asynchronous pattern of seed growth and development associated with the morphology of flowering in the family (Gray and Steckel, 1982). Because of this, and because the development of the capacity of seed to germinate is not always coincident with the attainment of maximum seed dry weight (Austin, 1972; Fussel and Pearson, 1980; Gray and Steckel, 1982; Gray _et_ _al_., 1984), the usual methods of determining seed maturity such as seed color, seed hardness and seed moisture content do not accurately predict seed maturity, unless changes in all of them are monitored frequently. Carrot seeds taken from parent plants were capable of germinating before the stage when maximum seed dry weight was reached, but even after seed moisture content had fallen below 20%, improvement in seed germination characteristics continued. Although seed germination was improved, 12 to 20 kg ha^{-1} of seed were lost every day due to seed shedding below 20% moisture content (Gray and Steckel, 1982).

Franklin (1953) recommended delaying carrot seed harvesting until tertiary umbel seed maturity, especially when it is safe to maintain the seed yield. Castra and Andrews (1971) reported an increase in seed yield as a result of delaying harvest until tertiary umbels reached maturity. However, they concluded that the overall effect of this practice was detrimental to the quality of mature seeds, because of the physiological deterioration caused mostly by adverse climatic conditions. Under the conditions of southern Idaho, Stallknecht _et_ _al_. (1982) reported a 50% loss of seed yield in carrot by delaying the harvest from mid-August to early September. Harvesting as early as August 1 and as late as September 9 did not affect germination of seed harvested from the primary and secondary umbels, while germination of seed from tertiary umbels was significantly lower at the early harvest date due to immaturity.

Austin and Longden (1967) showed that percentage of germination and to a greater extent, field emergence increased with later harvest. Under the conditions of the United Kingdom, Gray (1979) found that 'Royal Chantenay' carrot seed harvested on August 7 germinated 6 days earlier than those harvested on July 10. The mean time to germination increased with the umbel order, the delay in germination of seeds from the secondary umbels to those of the primary umbels was pronounced when harvest was made earlier. He also reported that germination responses were positively correlated to the seed embryo length (r=0.87). Weibe and Tiessen (1980) also reported good correlation between embryo length in the seed and earliness of emergence (r=0.92).

Clearly, it is desirable to delay the harvesting of carrot seed for as long as possible to allow embryo growth. Normally, this can be obtained only at the expense of some loss of seeds. But, William (1977) has shown that prevention of seed loss in many crops including carrots, can be achieved by spraying plants with a polyvinylacetate glue.

The CV of embryo length declined with a delay in harvest and the decline was greater for seed from the secondary umbels than primary umbels. Fewer seedlings emerged and the emergence was later from early harvested and secondary umbel seeds than from late harvested and primary umbel seeds. The CV of seedling weight was also decreased with a delay in harvest and was lower from seed from primary than from secondary umbels (Gray and Steckel, 1983).

Guy (1979) studied the relationship between maturity and germination of fennel seeds. He reported that immature seeds of fennel did not germinate, and to be capable of full germination, seeds need to attain the stage of physiological maturity recognized by the browning of the seeds. He added that embryos, where radicle and cotyledons have not been differentiated before harvest did not have any subsequent growth or germination.

Hawthorn et al. (1962) recommended 45 to 55 days from the appearance of the first flower to harvest for maximum yield and highest germination percentage in carrots. They reported that germination capacity of seed harvested 35 or more days after first flowers did not differ significantly between umbel orders. Brocklehurst and Dearman (1980) germinated carrot seeds harvested 44 and 104 days after anthesis. They found that mature seeds germinated 3 to 7 days earlier than the immature ones. High protein and nucleic acid content per unit dry matter as well as rRNA and poly(A)RNA accounted for the observed differences in germination rates between the two batches of seeds.

Carrot, parsley and onion seeds harvested at the green stage germinated poorly. Conversely, seeds harvested at pre- and full-ripening stages had higher germination percent (Anghel and Teodorescu, 1961). Early work by Borthwick (1931a) showed that failure of a large proportion of seed to germinate was due to immature embryos in carrot seeds. Similarly, Flemion and Uhlmann (1946) reported variable percentage of immature embryos in different crop seed lots. Celery had 14% and carrot and parsley had 4% immature embryos. The presence of a third kind of defective embryo in carrot seeds and other Umbelliferae, which is the rudimentary embryos, was also reported by Borthwick (1931a), Flemion and Uhlmann (1946) and Flemion *et al*. (1949).

In wild carrot seed, it was suggested that delayed germination could be imposed by a mechanical restriction on the embryo by the endosperm (Dale and Harrison, 1966).

Plant Density

The yield of seed in carrot is determined by the number of umbel heads produced per unit area. At low population (4 plants/m^2) many secondary and tertiary umbels are produced, but the number of these decreases as the plant population is increased to 8 plants/m^2 (Hawthorn, 1951b). Yield of seed increased rapidly with increased density from 4 to 8 plants/m^2, but remained steady for further increases to 20 plants/m^2 (Austin and Longden, 1966). Carrot seed quality expressed in the percentage of large seed and 500 seed weight improved with wider spacing (Malik, 1973). Seed yield per plant increased with wider spacing, while seed yield per unit area (ha or acre) increased with closer spacing (Seaton and Baten, 1940; Hawthorn and Pollard, 1954; Krarup and Montealegre, 1975).

One approach suggested for improving carrot seed quality without loss of seed yield was to modify the plant morphology by decreasing plant spacing (Gray, 1981, 1983). Low density in carrot seed crops allows the development of many lateral branches. At high densities, these branches are suppressed and the majority of seeds come from the primary umbels (Gray, 1983). Seed yield using root-to-seed method increased from 1100 to 1500 kg ha^{-1} as plant density increased from 100,000 to 800,000 plants ha^{-1}. At the highest density 60% of the seed yield was produced from primary umbels compared with less than 20% at the lowest density (Gray, 1981). A later study by Gray et al. (1983) showed that carrot seed yield increased by about 50 to 55% with an increase in plant density from 10 to 80 plants m^{-2} in two experiments, but in a third one, there was no effect of density on seed yield. The percentage of seed yield contributed by the primary umbel was similarly affected by density in two seasons and not affected the third season. These variations from year to year were later attributed to an increase in the spread of flowering time of the primary umbels caused by the increase in plant density (Gray and Steckel, 1985). Beside the effect on the spread of flowering time, high density planting increased lodging of the seed crop which resulted in substantial seed loss. The technique would be useful only for the seed-to-seed method because of the difficulty of transplanting the high root populations. This would eliminate steckling size-grading which has a significant effect on time to flowering and maturity (Gray and Steckel, 1980; Hawthorn, 1951b).

Pollination

The average seed setting in carrots under disease- and pest-free experimental conditions was estimated to be only 70% of its potential. Cross pollination was suspected to cause this limitation (Braak and Kho, 1958). During flowering, carrots and other Umbelliferous species are visited by a wide spectrum of insects as reported by Bohart and Nye (1960) and Flemion and Henrickson (1949).

Apis mellifera (honeybee) constituted only about one-third of visiting insects compared to syrphids which were the most abundant insects in a field of parsley grown for seed in Oregon. The highest yield (1620 kg ha^{-1}) in that field was obtained from open field plots exposed to all types of pollinators, compared to 1273 kg ha^{-1} from honeybees and 617 kg ha^{-1} obtained from plots where all pollinators were excluded (Burgett, 1980).

The importance of insect pollination in the production of good quality seed in carrots was emphasized by Bohart and Nye (1960), Franklin (1970), and Hawthorn *et al*. (1960).

Adequate and efficient pollination level, not only increased seed quality of carrots but gave very high seed yields. The average carrot seed yield of 4 years of experimentation with four levels of pollination, were 840 lb/acre in plots caged only with honeybee colonies and 711 lb/acre in open field plots, compared to 453 lb/acre in tiny insect pollination and only 178 lb/acre in plots where all pollinators were excluded (Hawthorn *et al*., 1956, 1960).

Diseases and Pest Damage

Arnott (1956) reported that outbreaks of a native plant bug *Lygus scutellatus*, which breeds on wild host species, dill and parsnips, were responsible for severe reductions in carrot seed yield in British Columbia. He also showed that bacterial blight caused by *Xanthomonas carotae*, aster yellow virus and root rots, were the most damaging diseases to carrot seed yield. Kenknight and Blodgett (1945) reported similar disease damage in Idaho. Both reports did not give the reduction extent that could result from these causes.

A population level of one lygus bug per umbel may reduce seed yield by 22.8% and germination by 25%, while 2 and 4 bugs per umbel caused 36.6 and 54.5% seed yield reduction, respectively (Scott *et al*., 1966). A reduction in total seed yield from 16 to 53%, depending on the stage of seed development was reported by Kho and Braak (1956). Feeding during blooming resulted in 44 to 62% seed yield reduction, while feeding after petal fall resulted in 22 to 31% reduction as estimated by Carlson (1956).

Scott and Homan (1968) reported an effective control of lygus by two applications of Dylox at 1 to 1.5 lb/acre. Chemical treatments in carrot and dill should begin when there are 1 or 2 bugs per umbel (Bech, 1966).

Detailed investigation by Flemion and her collaborators were entirely oriented towards the occurrence of embryoless seeds caused by lygus bug feeding on developing seeds and the Umbelliferae poor germination interrelationship. Seedlots of 16 different members of the Umbelliferae family were found to have embryoless seeds frequently and often in high percentage regardless of the seed source or the production area, i.e., Egypt, United States, or Norway (Flemion and Uhlman, 1946, Flemion and Henrickson, 1949). They reported averages of 8, 16, 20, 24, and 34% of embryoless seeds in the seedlots of celery, parsnip, carrot, parsley, dill and fennel, respectively. Although many reports attributed the occurrence of embryolessness to lygus spp. feeding (Arnott, 1956; Flemion and Olson, 1950; Flemion *et al*., 1949), it has been suspected that embryoless seeds could result from other undetermined causes (Robinson, 1954). In fact results of Flemion and Olson (1950) indicated that a relatively high percentage of embryoless seed in celery was obtained from insect-free caged plants.

Germination Inhibitors

The presence of germination inhibitors has been reported in seeds of most of the Umbelliferous crops. Chaturvedi and Muralia (1975) have extracted inhibitory substances from seeds of fennel, cumin, carrot, carum and corianders. They noticed differences in their effects as measured by germination, root length and hypocotyl length. Cumin and fennel were the most sensitive species among the five studied crops, and have higher inhibitory substances. Carrot and coriander were intermediate, while carum was the least sensitive with less inhibitory substance. Putievsky (1980) found that leaching and drying of caraway, coriander, and dill seed hastened their germination.

Inhibitory substances from carrot seed were extracted with ether, ethanol and hot water, with maximum inhibitory activity of germination obtained with the ether extraction (Aki, 1961). Purification of the extract gave a colorless oily extract. The most powerful inhibitory actions were obtained from the pericarp of immature seeds, with the maximum concentration reached after 41 days after flowering, with no changes in the later stages of seed maturation or during seed storage (Aki and Watanabi, 1962; Czysewski, 1958). The inihibitory extract from carrot seeds was named 'Carrotol' by Aki and Watanabe (1961). They showed that a dilution of 1/4000 was sufficient to inhibit carrot and lettuce seed germination.

Hormonal Regulation of Reproductive Development in Plants

Role of Gibberellins in Stem Elongation

The discovery and isolation of the gibberellins proved to be a major turning point in studies of stem elongation (Phinney and West, 1960; Sachs, 1965). Lona (1957) concluded that the process of stem elongation resulted from an increase in cell divisions in the "pith" (subapical) region; however, because of various plant responses which were similar between far-red light and GA, he concluded that GA is not the only factor controlling stem elongation. Sachs and Lang (1957) reported that cell division in the subapical region of non-vernalized *Hyoscyamus* increased almost 10-fold 24 hours after the application of 5 micrograms of GA. Sachs (1961) later showed that GA applied to fully vernalized *Hyoscyamus* increased stem height almost double that of vernalized controls, the difference in height due to both increases in cell length and number.

In another investigation, Sachs *et al*. (1959) emphasized the important role of cell division in the subapical zone in stem elongation. They observed within 24 hours after application of GA to rosette plants *Hyoscyamus* and *Samolus*, a marked increase in mitotic activity in all non-lignified tissues below the apical meristem. The induced subapical meristematic zone increased in size for several days commensurate with the increase in stem elongation. The new cell divisions were transverse, predominately oriented in long files. There was no observed effect of GA on cell division in the apical region and no evidence for cell elongation for at least 72 hours; therefore, the initial increase in stem length was due solely to the increase in cell number. A similar effect of GA was reported in the long-day plant, *Rudbeckia bicolor*, and the short-day plant, *Perilla nankinensis* (Bernier *et al*., 1964).

The subapical meristem is also responsible for stem growth in caulescent plants and may be controlled by gibberellin-like substances (Sachs *et al*., 1960). An extensive subapical zone of meristematic activity is normally present in caulescent plants. Growth retardants completely inhibit this activity, causing a rosette-type of growth without affecting leaf and flower initiation. Gibberellic acid prevents or reverses the inhibition of stem elongation caused by the retardants (Sachs *et al*., 1960; Sachs and Lang, 1961; Sachs and Kofranek, 1963). From these studies it was concluded that a function of gibberellins is to regulate the activity of the subapical meristem which is responsible for shoot histogenesis in caulescent as well as elongating rosette plants.

Influence of Giberellins on Flowering

Repeated applications of GA_3 caused flowering of LD rosette and LSD plants under SD and certain cold-requiring plants if grown under LD (Lang and Reinhard, 1961). Generally LD caulescent and SD plants were not induced to flower by gibberellins. Lang (1956a) first reported that gibberellin caused only stem elongation in Hyoscyamus, but when the plants were grown under LD flowering resulted (Lang, 1956b). Plants kept under SD elongated but remained vegetative. Centaurium minus Moench is a rosette plant, some forms of which require vernalization and other LD. Application of GA_3 was made to rosette plants until stem elongation had begun. Plants which were then grown under SD ceased to elongate and formed a new aerial rosette, but the plants under LD continued to elongate and flower (Carr et al., 1957). Thus, it was believed that gibberellin would replace the low temperature but not the LD requirement in these species.

Purvis (1960) demonstrated that gibberellins did not replace the low temperature effect on flowering in petkus winter rye but did stimulate stem extension. Lang (1956c) had earlier reported similar results. TsuKamoto and Konishi (1957) showed that small amounts of gibberellin applied at the beginning of vernalization accelerated stem elongation in radish but not flowering. Only high levels of gibberellin were effective in promoting flowering, the response being greater under LD than SD. If applied immediately after vernalization, gibberellin promoted stem elongation and consequently flowering in a number of other cold-requiring plants, e.g., carrot, parsley and turnip, only stem elongation resulted whereas others flowered (Lang, 1956c, 1957a). Wittwer et al. (1957) reported that gibberellin applied to cabbage caused stem elongation without flowering; however, in a number of other horticultural crops flowering did result (Wittwer and Bukovac, 1957; Bukovac and Wittwer, 1957).

Lona (1957) and Wellenseik (1960), using different experimental procedures and comparisons, showed conclusively that the role of gibberellin was promotion of stem elongation (particularly rosette plants) and that stem elongation and flower initiation do not always coincide. Wellenseik (1960) found no consistent relationship among the species tested (both biennial cold-requiring and photoperiodic plants), and concluded that in some plants a relation existed between stem elongation and flower formation, while in others there was no relation. Lang (1957b) had presented examples of other species showing only stem elongation without flowering.

Other experiments showed convincingly that stem elongation was not always associated with flowering. Margara (1960) reported that GA caused stem elongation but not flowering in unvernalized beets grown under 8- and 24-hr photoperiods. After complete vernalization, GA application (a) increased stem elongation if applied soon after vernalization, (b) had a small effect if applied when plants were already flowering, and (c) caused stem elongation under short day if completely vernalized beets were held under SD for 60 days (the minimum devernalizing period) and then transferred to continuous light, the plants remained vegetative. Gibberellin applications to these plants resulted in stem elongation but not flowering.

Most of the negative results obtained in flowering response to gibberellins were argued on the basis that the wrong gibberellin had been used. Michniewicz and Lang (1962) studied the effect of nine different gibberellins, GA_1-GA_9, on stem elongation and flower formation in cold-requiring, LD and LSD plants. Marked differences were established between gibberellins in their capacity to induce flower formation, but not all plants responded to the same gibberellin in the same way. Therefore, it is not possible to say gibberellins had no influence on a process if only one or a few were used. In a later study, Zeevaart (1963) reported that GA_3 and GA_7 induced stem elongation in the cold-requiring rosette plant *Lunaria annua* L., but not flower formation.

Effect of Growth Retardants

The use of growth retardants has provided another method of modifying plant growth. They have increased in importance from a practical, economic basis (Sachs and Hackett, 1972) as well as in physiological and biochemical studies on gibberellins (Cross, 1968). These compounds reduce stem elongation without disruption or alteration of apical meristem function or loss of apical dominance. The reduction of stem elongation is a response opposite to that of gibberellins, and can be completely reversed by the application of gibberellins.

The compounds commonly considered as growth retardants include (a) 2'-isoporpyl-4'-(trimethyllammonium chloride)-5'= methyLphenyl-piperidine-1-carboxylate(AMO-1618 or Acpc), (b) -cyclopropyl, -4-methoxyporpyl, -5-pyrimidine methanol (Ancymidol), (c) (2-chloroethyl,trimethylammonium chloride (CCC, Cycocel or Chloromequat), (d) 2,4-dichlorobenzyl-tributylphosphonium Chloride (Phosfon-D or CBBP) and (e) N-dimethylaminosuccinamic acid (B-995, Alar, or SADH) (Anon, 1972). The literature on these growth retardants was reviewed by Cathey (1964), including the history and development, structural requirements for activity, and effects on plants.

Effect on Stem Elongation

The effect of growth retardants on stem elongation was mentioned before in this chapter. Sachs (1961) and Sachs and Kofranek (1963) reported that AMO, CCC and Phosfon inhibited subapical mitotic activity in chrysanthemums and that application of GA_3 reversed this effect. Humphries and French (1965) observed that CCC flattened and GA_3 elongated the growing point of sugar beets. Zeevaart (1964) treated 3-day old seedlings of Pharbitis nil with CCC. At maturity of the stem, the CCC-treated seedlings contained one-third as many cells as the untreated. Stem elongation was retarded in chrysanthemums by SADH due to a decrease in cell division and cell elongation (Mitlehner, 1967).

Stem elongation was reduced but AMO and CCC did not affect leaf formation in Samolus (Baldeu and Lang, 1965). Alar (SADH) reduced stem elongation in various plants but did not affect leaf number

(Jaffe and Isenberg, 1965) nor flowering (Edgerton and Hoffman, 1965). Ancymidol reduced stem elongation not only on most of the species responsive to other kinds of retardants; but on many species that were previously non-responsive (Cathey, 1975). It appears that a definite response to the growth retardants is reduced stem elongation, attributable mostly to a reduction in mitotic activity and cell elongation. However, other developmental changes, such as leaf growth and floral initiation occur suggesting that the apex is still functioning.

The effect of these growth retardants has been shown to be reversed by GA_3 application. Reduction of stem elongation by CCC (Margara, 1961; Zeevaart, 1964; Baldeu and Lang, 1965a; Jones and Phillips, 1967), SADH (Jaffe and Isenberg, 1965; Zeevaart, 1966a; Picard, 1967), AMO (Baldeu and Lang, 1965a; Cleland and Zeevaart, 1970; Ende and Zeevaart, 1971), and Ancymidol (Leopold, 1971; Dicks _et al_., 1974; Suge, 1980) was reversed by GA_3. Inhibition of cucumber hypocotyl elongation caused by AMO, CCC, SADH, and Ancymidol was completely counteracted by GA_3 (Moore, 1967; Dicks and Abdel-Kawi, 1979).

Kuraishi and Muir (1963) tested CCC and Phosfon with auxin and GA_3 on radish leaf disc expansion, _Avena_ coleoptile section, and pea epicotyl section tests. They found that the growth inhibitor retardation was not reversed by GA_3 but was by IAA. Also, CCC-treated pea plants showed a marked decrease in amount of diffusible auxin from stem apices compared to normal plants. They concluded that the retarding effects by CCC was due to a lowering of auxin levels in the plant; however, they did not present any measurements of gibberellin levels. A later study by Leopold (1971) indicated that auxin-induced growth of *Avena* coleoptile sections was inhibited by Phosfon, while gibberellin-regulated growth of lettuce hypocotyls was uniquely inhibited by Ancymidol.

Cell division and expansion in tobacco, carrot, chrysanthemum, and geranium tissue cultured *in vitro* were inhibited by AMO, CCC and Phosfon (Sachs and Wohlers, 1964). Neither GA_3 nor IAA reversed the inhibition. Murashige (1965) reported that callus growth of tobacco tissue was suppressed by AMO, CCC and Phosfon and was not reversed by GA_3. Thus, it appears that exogenous GA is effective only on intact tissue and not on isolated plant parts.

Effect on Gibberellin Biosynthesis

Dennis *et al*. (1965), using ^{14}C-mevalonate and the endosperm of *Echinocystis macrocarpa* Greene (wild cucumber), reported that AMO inhibited the cyclization of geranylgeranyl pyrophosphate to (-)-Kaurene, an intermediate of gibberellin biosynthesis (Cross, 1968). Chlormequat (CCC) failed to inhibit (-)-Kaurene formation in this higher plant preparation, but in *Fusarium* it functioned like AMO, inhibiting the cyclization to (-)-Kaurene but not affecting the conversion of (-)-Kaurene to GA (Barnes *et al*., 1969).

The gibberellin content of pea seeds in excised pods was reduced by AMO. A concentration of 5 mg L^{-1} had no effect on growth of the seeds but gibberellin content was reduced significantly (Baldeu *et al*., 1965). This indicated that changes in gibberellin content in the seed was a consequence rather than the cause of changes in growth. The endogenous GA-like levels in seeds of Pharbitis nil were reduced when treated at anthesis with CCC (Zeevaart, 1966b), with no reduction in fresh and dry weight of the seeds. The progeny of the treated plant, however, have reduced endogenous GA-like levels (Zeevaart, 1966b; Felippe and Dale, 1968). Paleg et al. (1965) showed that AMO, CCC and SADH did not block the GA-induced release of reducing sugar from barley endosperm where GA was already present before addition of the retardants. This suggested that these compounds do not influence the action of gibberellin present in higher plants. Lang (1970) stated that the relation between the effect of growth retardants on inhibiting growth and GA biosynthesis is justified only if the effect of growth retardants can be completely overcome by exogenous gibberellin.

Alar (SADH) has been shown to retard stem elongation, decrease cell division and not affect leaf or flower initiation much the same as the other retardants, however, much less is known of its mode of action. Ninnemann et al. (1964) reported that SADH did not inhibit GA biosynthesis in Fusarium moniliforme. The compound was readily recovered from the culture and was therefore not metabolized or inactivated by the fungus. Reed et al. (1965) suggested the mode of action was in the inhibition of auxin synthesis. The inhibition of shoot elongation in dwarf and tall peas was related to reduced oxidation of tryptamine-2-^{14}C to indoleacetaldehyde-2-^{14}C; and in pea epicotyl homogenates, the action was attributed to the in vivo formation of 1,1-dimethylhydrazide which strongly inhibited tryptamine oxidation. However, they showed no data for the effect on auxin levels in plants. This theory has met with opposition based on the fact that exogenous GA_3 will reverse SADH inhibition (Zeevaart, 1966a; Picard, 1967; Moore, 1967) and exogenous auxin will not (Zeevaart, 1966a; Moore, 1967). Zeevaart (1966a) and Moore (1967) suggested that SADH interferred with gibberellin or other hormonal activities in the shoot apex. Dennis et al. (1965) reported that SADH did not inhibit (-)-Kaurene formation from ^{14}C-mevalonate in E. macrocarpa endosperm homogenate; however, Wylie et al. (1970) have reported that in root tips of peas SADH caused an increase of geranylgeranyl pyrophosphate, indicating a disruption of the gibberellin biosynthesis similar to AMO and CCC.

Undurraga and Ryugo (1970) found that SADH lowered membrane integrity allowing vascular contents to diffuse rapidly into the external medium. See and Foy (1982) reported an inhibitory effect of SADH on the activity of membrane-bound succinate dehydrogenase in the mitochondria isolated from hypocotyl of bean (Phaseolus vulgaris L.). This may be related to other sites of retardant-induced inhibition and with the kinetic studies of Moore (1967) supporting the theory that retardants affect different processes.

The advent of Ancymidol was the latest one among growth retardants. It inhibits the growth of a wide spectrum of plants by inhibiting stem elongation (Tschabold et al., 1970). It also inhibits gibberellin-stimulated growth and both inhibitions can be reversed by applications of GA (Leopold, 1971; Leopold and Wright, 1970; Tschabold et al., 1970). Leopold (1971) suggested that one mode of action of

Ancymidol involves the depression of reactions subsequent to the initial GA action. Cell-free enzyme preparations from pea shoot tips and wild cucumber (Marah oreganus) endosperm were used to test the effects of Ancymidol on the incorporation of mevalonic acid-^{14}C into Kaurene and Kaurenol, respectively (Coolbaugh and Hamilton, 1976). They found that Ancymidol (10^{-6}M) completely blocked the conversion of Kaurene to Kaurenol. At higher concentrations (10^{-3}M) Ancymidol inhibited the incorporation of mevalonic acid-^{14}C into Kaurene to a lesser extent. The effect of Ancymidol on GA biosynthesis by Gibberella fujikuro showed 97% inhibition of GA production, however, all Ancymidol concentrations affected the dry weight of the culture due to the fungitoxic nature of the chemical (Shive and Sisler, 1976).

Effect on Flowering

The level of endogenous gibberellins increased during low temperature treatment, particularly of seeds and in SD plants under long days. Chaila Khyan et al. (1963, 1967), in a comparative study of natural gibberellin content in rape, rye and wheat, showed that spring cultivars contained more gibberellins than winter cultivars, but that exposure to vernalization temperatures increased the gibberellin content to almost the level in spring cultivars. The levels of endogenous gibberellin-like substances were increased during low temperature treatment of radish seedlings (Suge and Rappaport, 1968) tulip bulbs (Aung and DeHertogh, 1968) and cauliflower plants (Thomas, 1972).

Qualitative and quantitative changes in the gibberellin-like substances have been reported. Aung and DeHertogh (1968) observed a large increase of the "free form" of gibberellin after 13 weeks of cold treatment. They concluded that both release from the "bound form" and synthesis occurred during the low temperature treatment. Other qualitative changes in gibberellin-like substances have been reported during cold treatment of broccoli (Fontes et al., 1970), the effect of photoperiod on red clover (Stoddart and Lang, 1967) and Silene armeria (Ende and Zeevaart, 1971) and metabolic interconversions in pea seedlings (Jones and Lang, 1968).

Since growth retardants have been shown to decrease gibberellin synthesis, their use in flowering studies may help to clarify gibberellin involvement in flowering, and their effects on the reproductive processes in higher plants. In the LSD plant Bryophyllum daigremontianum, Zeevaart and Lang (1963) observed that induction of flower buds occurred under SD following the required number of long days or GA_3 applications at night temperatures of 11 and 15°C but not 19°C. Chlormequat (CCC) inhibited floral initiation when applied under inductive conditions (Zeevaart, 1963). A very small amount, 1.5 mg plant^{-1}, of exogenous GA_3 reversed the suppression by CCC on flowering, but 10 times that amount was needed to completely reverse the reduction in stem elongation.

Baldeu and Lang (1965a) reported that in Samolus parviforus, a LD plant, AMO and CCC inhibited flower formation and stem elongation when applied under inductive long days. Small amounts of GA_3 reversed the effects of AMO, but the amount required increased as concentration of

AMO increased. Much larger amounts of GA_3 were required to reverse the CCC inhibition of stem elongation than that of flower formation. They stated that LD increased the level of endogenous gibberellins, but no determination was made of the endogenous gibberellin levels.

Application of CCC via the roots of SD *Pharbitis nil* during a 24-hr period prior to induction suppressed flower formation of the terminal buds (Zeevaart, 1964). If application is made after the induction period, flowering is not inhibited but stem growth is reduced markedly. Gibberellic Acid (GA_3) applied before the induction period revised the CCC suppression of flowering, but a considerably larger amount (50-100x) was required to overcome growth suppression. In another experiment using SADH, Zeevaart (1966a) obtained similar results. Inhibition of flower formation was caused by application of SADH to the plumules or cotyledons even if applied after the inductive night. Only 0.01 mg GA_3 $apex^{-1}$ was needed for reversal of flower suppression, but 10 times that amount was needed for normal internode length. Exogenous IAA and NAA were inactive in reversing the SADH effect.

In a later study, Suge (1980) reported that inhibition of flower formation and growth in *Pharbitis nil* was caused by Ancymidol application via the cotyledons or roots prior to inductive dark period. Inhibition of flower formation was completely reversed by GA_3 application to the plumule before the inductive dark period. A dose of 0.01 mg GA_3 $plant^{-1}$ was sufficient to restore flowering, but about 100 times more GA_3 was required to restore the internode length to that of control.

Species of the LD rosette plant Hieracium responded to GA_3 and $GA_{4/7}$ similarly as the other LD species (Peterson and Yeang, 1972). Exogenous GA_3 on plants under SD produced stem elongation but no flowering. Growth retardants AMO and CCC reduced stem elongation but did not affect flowering.

Application of AMO, CCC, Phosfon and SADH applied to winter wheat during seed vernalization inhibited ear development (Suge and Osada, 1966); however, the retardation was not complete. Chlormequat (CCC) reduced flowering only when marginal cold treatments were given and there was no stem growth. If applied after the cold period, CCC reduced stem height but did not affect flowering. Michniewicz (1966) reported that CCC decreased the response of winter wheat when applied before vernalization.

Margara (1961) observed that allyl trimethylammonium bromide, an analog of CCC, reduced stem elongation if applied to beets after the required cold treatment. Flower formation was retarded but not inhibited. Inhibition of stem elongation could be overcome by GA_3 application.

Application of CCC before vernalization of a Japanese cultivar of radish seeds inhibited bolting slightly but was more effective if applied after vernalization (Suge and Rappaport, 1968). This retardant did not inhibit flowering but did reduce the level of gibberellin-like substance when applied during or after vernalization. Exogenous GA_3 and GA_7 caused all non-vernalized plants to bolt but not flower when grown under non-inductive conditions in the greenhouse. When grown in growth chambers, all non-vernalized plants grown under

SD (8 hrs), with or without GA_3, did not flower; however, GA_3 caused bolting in all plants under both SD and LD (16 hrs). These results indicated that gibberellins have a direct influence on seedstalk elongation but were not directly functional in flower initiation.

It can be concluded that exogenous GA caused flowering in certain LD and cold-requiring species, with rather large doses required to stimulate or replace vernalization. Long days as well as low temperatures resulted in increases of exogenous gibberellin-like substances. Growth retardants decreased gibberellin-like activity and stem elongation but seldom affected flowering. Larger amounts of GA were needed to reverse the inhibition by retardants on stem elongation than flowering.

Effects of Growth Regulators on Flowering and Stem Elongation in Carrots

Immediately after the initial observation that gibberellin replaced the low temperature requirement of a biennial plant (Lang, 1956b), several investigators reported the same response for carrots (Lang, 1956c; 1957a; Bukovac and Wittwer, 1957; Harrington and Rappaport, 1957; Wittwer and Bukovac, 1957). However, the response in hastening the flowering process was possible only after large amounts of GA were applied, after prolonged treatments with GA or when the temperature was maintained near the threshold for induction (Lang, 1957b; Wittwer and Bukovac, 1958).

Lang (1956c, 1957a) reported that some but not all plants of the 'Early French Forcing' cultivar formed flowers after 1-1/2 to 1-1/2 months of daily applications of 10 mg GA whereas the cultivar

'Danver's Half Long' only gave a bolting response. Bukovac and Wittwer (1957) made weekly application of 10 to 20 mg GA for 10 successive weeks to nonvernalized carrots grown at 6°C (60°F). Gibberellic Acid (GA_3) did not increase the percentage of plants which flowered; however, 25% of the plants which received no GA flowered as well. The first visible flower in those plants which flowered with no GA appeared within 83 days, whereas those receiving 20, 50, and 100 mg GA $plant^{-1}$ appeared in 93, 95, and 94 days, respectively. Also, seedstalk height, measured when the flower primordia appeared was 27 cm for no GA and 61 cm for 100 mg GA.

Application of five to six treatments of 100 and 1000 ppm GA starting at the 6 to 8 leaf stage induced stem elongation and flowering if the greenhouse temperature was maintained near 55°F (Dickson and Peterson, 1960). However, the reproductive phase was incomplete in some plants, because no flowers developed on the tall stems or were abnormal and did not set seed. Globerson (1972) showed that soaking nonvernalized mature roots in a solution of 100 ppm GA_3 induced flowering, under 46 to 52°F temperature regime.

Harrington and Rappaport (1957) reported that GA application to vernalized carrots hastened the flowering process. Dickson (1958) observed that GA_3 application complemented partial cold treatments for stem elongation. With either partial or complete vernalization, GA_3 application increased the height of seedstalks often 2-1/2 times the normal height. If the seedstalks were exceptionally tall, flowers were sometimes abnormal or not even formed, which resulted in a "vegetative" seedstalk (Dickson, 1958).

Hiller et al. (1979) reported that after 10 weeks vernalization at 5°C, high greenhouse temperature (32/27°C) (day/night) severely reduced seedstalk height in three carrot cultivars. Endogenous gibberellin-like activity was also decreased. At low temperature (21/15°C), gibberellin-like activity remained fairly constant during the 10-week sampling period. They showed that changes in endogenous gibberellin-like activity were related with stem elongation, but not with floral initiation. Application of exogenous GA_3 (1000 ppm) following vernalization prevented the inhibitory effect of high greenhouse temperature on seedstalk elongation, and resulted in seedstalk heights comparable to untreated control grown at low temperature. Exogenous application of SADH and CCC at 5000 ppm and 1500 ppm, respectively, reduced seedstalk height of plants at medium (27/21°C) and low temperature to that of untreated controls grown at high temperature.

In a recent study, Nieuwhof (1984) reported that application of GA_3 to nonvernalized carrot plants promoted stem elongation especially under high temperature conditions. Plants which bolted after GA_3 application deviated from normal bolters by formation of a short thickened stem, with occasional flower formation. Gibberellin (GA_3) applied at a lower vernalizing temperature (10°C) inhibited flowering.

The above results indicate that carrots respond more readily to GA when grown near threshold induction temperature and those cultivars flowering normally after GA applications are the ones which appear to have a smaller vernalization requirement. Stem elongation but not always flowering results from GA treatment. Thus it appears that the primary effect of gibberellin in carrots is on stem elongation.

Effect of Growth Regulators on Seed Development and Germination

The role of growth regulators in seed development and germination is far from being understood, in spite of the well known fact that developing seeds contain high concentrations of some growth regulators. Many seeds have the capacity to synthesize gibberellins and convert one form of GA to the others (Radley, 1976). *Pisum sativum* seeds showed large increases in cytokinin-like substances when grown in culture (Hahn *et al*., 1974). Many seeds contain ABA and other germination inhibitors. Milborrow and Robinson (1973) showed that both the embryo and endosperm of wheat were capable of de novo synthesis of ABA from applied mevalonic acid. Ihle and Dure (1970) have postulated that ABA is synthesized in the ovules of cotton fruit and then transported to the embryo during embryogenesis.

Gray and Thomas (1982) concluded that during seed development and maturation many seeds import hormones from the parent plants, besides having the capacity for in situ synthesis of certain hormones. Based on that, derivation of seed hormones must have important implication when considering the application of growth regulators to improve seed production, particularly in relation to the optimum time of application.

Pre-Flowering Application of Growth Regulators

Application of growth regulators before flowering is aimed primarily towards floral induction and regulating the numbers of flowers produced by a plant (Gray and Thomas, 1982). An increase in seed yield, mainly by affecting the number of seed produced, and improvement of seed quality might be expected from such application.

Supplementation of cold treatment by growth regulators sprays improved flowering of many biennial plants, particularly when the minimum cold requirement has not been achieved. Application of GA_3 to carrots (Globerson, 1972), onion (Cogran and Montano, 1975) and kholrabi (Van Marrewijk, 1976) and cytokinins to brussels sprouts (Thomas, 1976) improved flowering, seed production and quality, in partially vernalized plants. Foliar applications of either BA or N-4-pyridyl-N'-phenylurea (NC5392) to brussels sprouts, increased the number of plants flowering and stimulated the flower stalk development on those plants which responded to a short low temperature treatment (Thomas, 1976). The number of siliques per plant was increased by NC5392 but not by BA, and while NC5392 had no effect on seed number per silique, BA caused considerable reductions. Seed weight was little affected by chemical treatment, but the percentage of these seeds under optimum conditions was about twice those from untreated seeds.

Application of daminozide at 4000 mg L^{-1} to brussels sprout plants prior to vernalization decreased flower stalk height, increased seed yield per plant and improved total percentage germination (Thomas and O'Toole, 1980). Average seed weight was unaffected indicating no evidence of increased hormone-controlled assimilate movement to individual seeds. Treatment of lettuce plants with soil-drench application of 2000 mg L^{-1} chlormequat chloride reduced the length of flower stalk, delayed flowering and seed ripening, but considerably increased the percentage of germination of the harvested seeds (Thomas, 1968). However, the yield of seeds from treated plants was considerably lower than that from control plants, and some of the growth-retarding effect of the chemicals were apparent in the progeny seedling. Results obtained with arrowleaf clover (Ball *et al.*, 1974), onions (Crogan and Montano, 1975; Levy *et al.*, 1972; Naamni *et al.*, 1980), carrots (Globerson, 1972), lettuce (Globerson and Ventura, 1973) and cauliflower (Singh *et al.*, 1976) support the suggestion that pre-flowering growth regulator applications mainly affect seed yield and often quality rather than seed size.

Application of Growth Regulators During Seed Development

Application of growth regulators during seed development is likely to affect seed yield and performance, mainly by altering seed size, hormonal balance, though seed number could be altered through effects on subsequent ripening and abscission (Gray and Thomas, 1982). Increases in seed size, vigor or germination have been reported following application of naphthalenacetic acid (NAA) to sugar beet (Malik and Shakara, 1977) and wild oat (Hurt *et al.*, 1977), GA to rice (Mukherjee and Prabhakar, 1980), daminozide to red clover (Hulewicz *et al.*, 1975) and ABA, GA and CCC to *Lactuca scariola* (Gutterman *et al.*, 1975). In *Lactuca scariola*, treatment of plants during flowering with

ABA, GA and CCC markedly affected seed size, germination and endogenous GA levels in different ways, but all the chemicals improved germination and both GA and CCC increased extractable GA levels.

Application of Growth Regulators During Seed Maturation

Thomas et al. (1978) demonstrated in celery that growth regulators, namely daminozide or ethephon treatments given during seed maturation, alleviated the dormancy of the later-formed (tertiary and quaternary) seeds, so allowing the whole population of seeds to germinate over a shorter period of time. Further experiments with celery (Thomas and O'Toole, 1981) confirmed the beneficial effect of growth regulator sprays during seed maturation on dormancy-break and germination. The most effective treatment was a mixture of $GA_{4/7}$ with ethephon, however, the effects of these sprays were less apparent and inferior to those obtained by soaking the harvested seeds with the same mixture.

Reproductive Responses of Plants to Temperature Stress

Microsporogenesis as Influenced by Temperature Stress

Downes and Marshal (1972) have demonstrated that exposing sorghum plants to night temperature of 13°C or less during meiosis was critical and can induce male sterility. Brooking (1976) reported induction of male sterility in grain sorghum by exposure of plants to five low temperature nights (25/10°C). He found greater sensitivity at the late archesporial cell, pollen mother cell (PMC) developmental stage up to the laptotene stage of meiosis. Sterile pollen at anthesis was found devoid of starch and had low level of proline. In his studies, female fertility was, however, unaffected.

Brooking (1979) further studied genotypic difference in sensitivity to low temperature in sorghum. Three genotypes were compared for low temperature during the laptotene stage under treatment regimes of 21°C day and 14, 11, 8, and 5°C night. A sensitive hybrid showed progressive reduction in pollen proline level, percentage starched pollen with decreasing night temperature. He observed, however, that pollen fertility was still sufficient to enable near complete seedset in all treatments.

Gonzalez (1982) reported pollen abortion and anther shrinkage in grain sorghum when temperature was increased. Pollen did not stain and showed no starch accumulation under high temperature stress. In male sterile lines of sorghum (Raj, 1968), degeneration was observed at different stages such as PMC, dyad, and tetrad and even at the developmental stages of microspore after normal tetrad formation.

Induction of floret sterility by low temperature in millet was reported by Mashingaidze and Muchena (1982). They found that pollen grains were shrivelled, degenerated, vacuolated and were devoid of starch and cytoplasm due to low temperature (min. 11.2, 13.6, and 14.1°C) under field conditions. Low temperature during booting delayed anther emergence and also led to indehiscent or empty anthers.

The response of rice to low temperature treatment is detailed by Japanese workers since 1949. Sakai (1949) reported sterility in rice due to abnormal hypertrophy of tapetal cells caused by low temperatures. The effect of cool temperature on microsporogenesis was reported in a series of experiments in rice during the 1970s. Ito et al. (1970) reported a decrease in the rate of pollen germination on stigma and pollen grains stained weakly with acetocarmine. An increase in frequency of anthers remain in inside spikelets due to cool treatments (12°C) for 2 to 4 days was observed. They observed non-fertilization of ovary due to incomplete anther development, pollen immaturity and anther indehiscence in rice plants subjected to severe cooling for 4 days. The percentage of fertilized spikelets was decreased by less than 50% of the control when treated at the meiotic stage (Nishiyama, 1970).

Satake and Hayashe (1970) and Satake (1976) found the most sensitive stage to coolness (12°C for 4 days) to be the young microspore stage from the tetrad to the first contraction phase in rice. Elongation of anthers was much delayed during cool temperatures but recovered to normal rates soon after transfer to warm temperatures. Field surveys in California have shown that 12.5% of the rice crop loss was due to low temperature-induced floret sterility (Board, 1979). The sensitive stage was reported to be microsporogenesis, 10 to 14 days before heading, when the panicle is enclosed in the sheath of the flag leaf. A critical temperature was found to be 15.5°C.

Attempts have also been made to study the effects of high temperature (35, 38, and 41°C for 8, 8 and 4 hrs for 5 days, respectively) on sterility of Indica rices at flowering by Satake and Yoshida (1978) under greenhouse and phytotron conditions. Spikelet sterility was induced by high temperature at flowering. High temperature during anthesis was most detrimental followed by time before anthesis. The major causes of sterility were abnormal pollen shedding and decreased pollen viability. Ability of the pistil to be fertilized appeared to remain unaffected by high temperature up to 41°C. Exposure of spikelet to 36.5°C for 8 hrs a day induced 20% sterility for N22, a heat tolerant genotype, while a treatment at 32°C was enough to induce sterility in a heat susceptible genotype. Two hours of treatment at 41°C induced 90% sterility in all the varieties.

Induction of abnormal sporogenesis in wheat by short periods of high temperature (30°C) at meiosis was reported by Saini and Aspinal (1982). High temperature treatment applied for 3 days at meiosis and tetrad break was found to lower grain yield through drastic reduction in grain set, but no effect was seen when high temperature was imposed during other stages of growth.

Herrero and Johnson (1980) studied pollen viability under high temperature stress in maize. They exposed tassels at the beginning of anthesis to day temperatures of 27, 32, and 38°C. Night temperatures were 6°C lower. *In vitro* germination of pollen showed a steady decrease in pollen germination as temperature increased in some genotypes. All genotypes had lower germination at 38°C than at 32 or 27°C and several genotypes exhibited no germination after 48 hours at 38°C.

Pollen sterility can be readily developed in tomato with excessively low or high temperature (Smith, 1932) under field conditions. The relation of temperature to blossom drop was similar to the relation of temperature to anthesis.

Further, a report on control of male sterility due to variation in temperature regimes in tomato was published by Sawhney (1983). He observed that a male sterile stamenless-2 mutant of tomato produced abnormal stamens and non-viable pollen at relatively intermediate temperature conditions (23/18°C). If mutant plants are grown at relatively low temperature (18/15°C), most flowers produced normal stamens with viable pollen. In contrast, he observed that plants grown at a high temperature (28/23°C) produced carpel-like structures in place of stamens with no evidence of pollen formation. However, the three temperature regimes had no effect on the pollen viability of wild type tomato plants. Weak light or low temperatures were reported to alter the structure of tomato flowers. They prevented dehiscence of the anther at the time the stigma was growing through the anther ring (Howlett, 1936).

Chang and Struckmeyer (1976a) found that the temperature under which onion plants were grown had a significant influence on pollen germination. Pollen collected from plants grown at 24°C had significantly higher germination than those from plants grown at 35°C. And at 35°C pollen germination was significantly higher than at 43°C.

Kuo _et_ _al_. (1981) reported that temperatures below 16°C or above 28°C reduced pollen germination and pollen tube growth in Chinese cabbage. Both male and female gametogenesis were affected by high temperature, but the most drastic effect of high temperature occurred after pollination.

Warrag and Hall (1984) demonstrated in cowpea, that the stage of floral development most sensitive to high night temperature occurred 5 to 7 days before anthesis. This corresponded with the stage just after the release of the tetrad from the microspore mother cell sac. In vivo germination of pollen from plants at 33/22°C was four times greater than that of pollen produced at 33/30°C.

Megasporogenesis as Influenced by Temperature Stress

Cell division during fertilization is a function of temperature like any aspect of growth in plants. Martin (1914) reported enhanced egg cell division in 18 hrs during high temperature as against 35 to 50 hrs required in cool temperatures for some legumes. In *Monotropa uniflora*, complete suppression of fertilization occurred at 8 to 10°C (Shibata, 1902, cited by Pope, 1943).

Endosperm nuclei in barley divided two to three times in 6 days at 5°C and eight times in a day at 30 to 35°C. No division in embryo was seen in 6 days at 5°C, but seven divisions were observed in 2 days at 30 to 35°C. However, no endosperm division was found at 40 and 45°C (Pope, 1943).

Dhopte (1984) reported ovule abortion in grain sorghum when plants were subjected to cool (17°C) or high (29°C) night temperatures, at 7 days after floret differentiation (FD + 7) stage. The percentage abortion was 30 and 33% at 17 and 33°C, respectively. This was associated with separation of integuments of the micropylar end and the degeneration of nucellus at the chalazal end. An increase in poorly developed pistils and shrivelled stigmas by 34 and 20% was noticed in cooler and elevated temperatures, respectively.

The regression in filament and pistil development due to high temperature (30 to 35°C) was reported in Citrus unshin by Takagi et al. (1982). They found slender ovaries in treated plants, and occurrence of abnormal fruit at high temperatures due to vigorous growth of the pedicel end. They also reported higher growth rate of the ovary wall due to high temperature.

In an attempt to evaluate blossom drop in tomato, Smith (1932) found increased blossom drop caused by hot dry winds and low humidity. Embryo sacs of aborting pistils never developed beyond a very weak egg cell stage in hot temperatures ranging from 15.6 to 23.9°C.

Young (1923) claimed that degeneration in the ovules and embryo sacs in potato results from unfavorable environmental conditions. He observed that in the late megaspore stage, blasting was accompanied by shrivelling of both the megaspore or embryo sac and cells of the nucellus.

Ormrod et al. (1967) observed retardation in embryo sac development in beans due to low temperature (24/15.5°C) under greenhouse conditions. The endosperm was never found to develop in cool temperatures. Similarly, high temperature (35/26.5°C) resulted in a lower proportion of normal embryo sac indicating its degeneration. They positively demonstrated that embryo sac development in beans is a temperature-dependent process.

The development of megagametophyte in onion showed no differences when plants were kept at 24, 35 or 43°C (Chang and Struckmeyer, 1976b). However, fertilization was severely affected by temperature treatments. One day after pollination, 50% of the ovules were fertilized at 35°C compared to 17 and 9% at 24 and 43°C, respectively, indicating that pollen tubes grew faster at 35°C than at 24 and 43°C. The overall average of percent fertilized ovules was 72 and 70% for 24 and 35°C, respectively, compared to 46.6% at 43°C.

The effect of temperature on endosperm development in onion was also investigated by Chang and Struckmeyer (1976b). At 43°C, the division of the endosperm nuclei of a fertilized ovule was retarded and only one or two continued to divide at a normal rate, compared to that at 35°C where 89% of the endosperm nuclei divided at a normal rate. At 24°C growth of the endosperm was slower and the endosperm of fertilized ovules also was more retarded than at 35°C. Ovary growth and zygote division were also more conspicuous at 35°C than at 24°C and 43°C.

Effects of Temperature Stress on Seed Yield

Temperature influences growth and therefore influences potential productivity of crops. Spikelet number in wheat decreased with an increase in temperature over a range from 10 to 30°C (Friend, 1965). Similar results reported by Halse and Weit (1974) showed that spikelet number was lower in plants grown in more extreme temperature regimes both low (10/5°C, day/night) and high (26/21°C) than in plants grown in moderate conditions of temperature.

In many instances, high night temperatures during reproductive development have been more detrimental to seed yield than high day temperatures. When night temperatures were raised approximately 10°C above ambient, seed yields were reduced in corn, wheat, and soybean by about 40, 45, and 10%, respectively (Peters et al., 1971). In sorghum, 25 to 36% seed yield reduction was reported when night temperatures were raised about 5°C above their optimum, and at 10°C above optimum, yield reductions were about 50% (Downes, 1972). A significant reduction occurred in seed number per plant (68%) and seed yield per plant (64%), when sorghum plants were exposed to high night temperature (24°C) at floret differentiation (FD) stage. These parameters were significantly reduced at cooler temperatures (17°C) only when treatments were imposed at FD + 7 day stage (Dhopte, 1984). Similarly, Eastin et al. (1983) reported 25 and 50% seed yield reduction in two sorghum hybrids when night temperatures were elevated about 5 and 10°C, respectively, above optimum.

Adverse effects of temperature on reduction in pod number were reported in cowpea (Summerfield et al., 1976). Day/night temperatures of 33/19°C resulted in lower seed yield in cowpeas compared to the effect of day/night temperatures of 27/19°C (Stewart et al., 1980). In contrast, Warrag and Hall (1984) found no influence of day air temperature on seed weight and seed yield in cowpea, however, seed shape and vigor were adversely affected by high day temperature.

Lupinus angustifolius growth was poor at temperatures above 27/22°C, and 21/16°C was the most suitable temperature for seed development (Downes and Galdestones, 1984b). In pearl millet, the number of grains produced declined as temperature increased from 21 to 31°C, but at 19°C only a few grains were produced. Mean grain weight increased as temperature decreased from 31 to 19°C (Ong, 1983).

Maturation of peas in cool temperatures (mean 17°C) led to the development of larger seed that gave larger plants, in comparison to those of the same varieties which had matured in warmer temperatures (mean 24.5°C) (Kant et al., 1983).

The influence of temperature on seed development in onion has been reported by Chang and Struckmeyer (1976b) who found that the optimum temperature for ovule and seed growth was about 35°C. Temperature in excess of this induced abortion of young seeds so that at 43°C there was 66% abortion.

The developmental stage at which plants experienced temperature stress has a profound effect on seed yield. Seed yield reductions were paralleled, in most cases, with declines in seed number, suggesting a deleterious effect of temperature during early flower development. Downes (1972) demonstrated that a high temperature (33/28°C) late in panicle development stage in sorghum induced floret abortion. Similar findings on the effect of heat stress on seed yield in sorghum were reported by Pasternak and Wilson (1969) who reported yield reduction from 10 to 20% due to heat stress at or soon after boot stages.

The greater the proportion of the reproductive period chickpea plants spend in hot days (35°C) the smaller the seed yield produced (Summerfield et al., 1984). They showed that transferring chickpea plants at 50% flowering from a diurnal temperature regime of 30/10°C virtually eliminated seed formation in the plants. Plants that spent at least 80% of the reproductive period in hot days were barren, while those which experienced hot days for about 60 or 40% of the postflowering period produced about 80 and 60% less than the control. Only plants close to reproductive maturity were able to escape thermal stress.

Seed yields were diminished when Chinese cabbage plants were transferred to high temperatures (34 to 37/22 to 24°C, day/night) at first anthesis or immediately after pollination stages compared to bolting, macroscopic appearance of flower bud or control (29/18°C). The most drastic effect of high temperatures on seed yield occurred when plants experienced high temperatures after pollination (Kuo *et al.*, 1981).

High day temperatures (33°C) before flowering prevented early flowers of *Lupinus angustifolius* plants from developing pods, but later flowers were able to compensate. High temperatures at flowering substantially reduced the number of pods containing seeds, with very little compensation in later podset or seed number. After flowering, high day temperatures did not affect the most developed pods, but seed production in the less developed pods was reduced due to ovule abortion (Downes and Galdestones, 1984b). Temperature regimes before flowering determined growth of the inflorescence for the first 24 days after flowering, but the ultimate seed yield was affected by conditions after flowering.

High temperature (33/28°C) during vegetative, stem elongation or grain development of pearl millet lowered grain yield by reducing tillering, number of grain/inflorescence and single grain weight. Low temperatures (21/16°C) during the vegetative stage increased basal tillering, and as a result total grain yield plant^{-1}; however, low temperature during stem elongation reduced spikelet fertility and inflorescence length and thereby reduced grain yield (Fussel and Pearson, 1980). Jones *et al*. (1984) showed in *in vitro* studies with maize that temperature extremes (15 or 35°C) during endosperm cell division (lag phase) or the effective grain fill period (EGFP) reduced final kernel mass, however, an unfavorable thermal environment during the lag phase caused the most reduction. Detrimental effects sustained in the lag phase prevailed when kernels were transferred to a more conducive temperature (30°C) during EGFP.

Influence of Temperature Stress During Seed Development on Seed Vigor

The influence of temperature during seed development on germination of tobacco was studied by Thomas and Raper (1975a). Germination was similar regardless of the temperatures during seed maturation. Rate of emergence, however, was 1 to 2 days slower and seedling growth was reduced by 17% when seeds matured at 33/26°C compared to 22/18°C or 26/22°C. When a low temperature (18/14°C) was imposed on tobacco plants during vegetative growth, seed germination was 14% less than those grown at the higher temperatures (22/18°C to 33/26°C) (Thomas and Raper, 1975b).

Exposure of spring wheat (*Triticum aestivum*) plants to low temperatures (<14°C) during the milk-ripe stage of seed development significantly reduced the requirement for vernalization (Kostjucenko and Zarubailo, 1937). Progeny plants grew and developed more rapidly when seeds matured at 15.5°C instead of 26.5°C (Riddell and Fries, 1958).

Day/night temperature treatments (25/20°C, 20/15°C, and 15/10°C) during seed development of Italian ryegrass (Lolium multiflorum), perennial ryegrass (Lolium perenne), and meadow fescue (Festuca pratensis) significantly influenced seed germination and vigor (Akpan and Bean, 1977). The germination percentage was the highest in seeds which developed at 25/20°C, especially at germination temperatures of 13 to 20°C. Seeds from the 15/10°C treatment germinated 2 to 3 days later, but produced seedlings with 20 to 24% more dry weight than those which developed at higher temperatures (25/20°C and 20/15°C). In pearl millet (Pennisetum americanum), seed viability and field emergence were unaffected by the temperatures (33/28°C, 30/25°C, 27/22°C and 21/16°C) at which the seeds developed. However, seeds which developed at 21/16°C produced seedlings with 40 to 60% more height and dry weight than those at 33/28°C (Fussel and Pearson, 1980). Cardinal temperatures for germination of millet seeds were unaffected by the temperature during seed development, however, the conditions during seed development did affect seed size, seed viability and germination rate (Mohamed et al., 1985). Studies on a non-dormant population of wild oats (Avena sativa) indicated that temperature treatments during vegetative growth (Sawhney et al., 1985), seed maturation (Sawhney and Naylor, 1980) and during the period immediately following maturation (Sawhney et al., 1984) significantly affected seed dormancy.

Soybean plants which matured in hot weather (32°C) produced seeds with lower germination and field emergence than those produced in cool weather (Green et al., 1965). Seedling growth and seed yield in the progeny of soybean were reduced by high temperature (27°C) during the last 45 days of seed maturation compared to those produced under low temperature (21°C) (Harris et al., 1965). Seed germination was delayed and seedling growth was reduced in pea when the mother plants experienced high temperatures (35°C) during the 10-day period after the pods had started to wrinkle compared to those which developed at 30°C (Harrison and Perry, 1973). Seeds of cowpea (Vigna unguiculata) which developed under high temperature 33/19°C exhibited high percent emergence when sown at a depth of 2.5 cm. However, 5-cm sowing resulted in poor emergence compared to those which developed at low temperature (27/19°C) (Warrag and Hall, 1984). Siddique and Goodwin (1980a) subjected 10 genotypes of bean to six temperature regimes (33/28°C to 18/13°C) from anthesis to seed maturity. All genotypes produced seeds of higher vigor at the low temperatures (21/16°C and 18/13°C) than at the higher temperatures (33/28°C and 30/25°C). Resistance to mechanical injury increased in seeds which developed under low temperatures. Seed size and vigor decreased linearly as temperature increased from 21/16°C to 33/28°C during seed development and maturity (Siddique and Goodwin, 1980b).

Seeds of bracted plantain (Plantago aristata) which matured at high temperatures (26/20°C) weighed less than those which matured at low temperatures (20/14°C) (Alexander and Wulff, 1985). Seeds which matured at high temperatures had a higher probability of germinating and a more rapid growth compared to seeds which matured at low temperatures (Stearn, 1960; Alexander and Wulff, 1985). The effects of maternal temperatures on seed weight, percentage germination and germination rate were detectable in a second generation.

Germination and emergence of spring-sown bulb onions were better from seeds grown in "warm" than "cool" years (Austin, 1963). Similarly, percentage germination of seeds were slightly, but significantly, improved by growing the seed crop at 20 to 30°C than at 15 to 20°C (Brewster, 1982). Recently, Gray and Steckel (1984) showed that seeds from onion crops grown at mean temperatures above 18°C gave higher percentage germination, when imbibed at 30°C than at 20°C, higher percentage seedling emergence and higher seedling weight than seeds from crops grown at lower temperatures. Seed germination of red beet decreased by 50% and the plants yielded 13% less when the mother plant was exposed to low temperature (12°C) during seed development compared with those exposed to higher temperatures (18 and 24°C) (Heidi *et al*., 1976). When cotton plants matured at night temperatures of 11, 15, 21, and 27°C in the growth chamber, 20 to 70% less seedlings emerged and the resultant plants yielded 20% less cotton in the field from seeds which matured at 11 and 15°C than at 21 and 27°C (Quisenberry and Gipson, 1974).

The Effects of Temperature on Flowering in Carrots

Sakr and Thompson (1942) reported that a 10 to 15°C greenhouse growing temperature following vernalization resulted in 60 to 100% flowering and was more favorable for reproductive growth in the cultivar 'French Forcing' than 15 to 21°C or 21 to 27°C. However, their data showed that flowering was not significantly different at 15 to 21°C or even 21 to 27°C compared to 10 to 15°C after a vernalization period of 60 days at 5°C. Only 20 to 40% of the plants flowered at growing temperatures of 70 to 80°F when the induction period was 2 to 4 weeks. This may indicate a devernalization effect, although it occurred primarily after short induction periods.

Dickson and Peterson (1958) found that plants at 55°F bolted earlier and in significantly higher percentages than those grown at 65°F following cold storage of the roots. They further reported that, if after the low temperature induction period carrots were grown in the 55°F greenhouse until seedstalks became evident, the reproductive cycle was hastened by raising the temperature to 70 to 80°F, but that the seedstalks were shorter compared to plants left in the 55°F greenhouse. Taller seedstalks were observed in plants grown at 55°F than 65 to 70°F (Dickson, 1958).

Percentage of plants flowering was reduced when the plants were exposed to 3 to 5 days of 21°C immediately after vernalization followed by 32°C for 3 to 5 days (Fisher, 1956). As growing temperature after vernalization increased from 10 to 15°C to 21 to 27°C, flowering was hastened, the degree of petaloidy was increased and plant height was decreased in two carrot inbreds, two hybrids, and the cultivars 'Royal Chantenay' and 'Danver 126' (Eisa and Wallace, 1969). Some plants of the cultivar 'Royal Chantenay' placed immediately at 21 to 27°C after 7 and 15 weeks vernalization were fully devernalized and remained vegetative, and others produced only a main umbel without stem elongation, i.e., a sessile flower.

Quagliotti (1967) reported for the cultivar 'Amsterdam Forcing' an inverse relationship of seedstalk height with temperatures, 26, 20, and 14°C, when imposed on the plants after seedstalk development had begun. As temperature increased the rate of seedstalk growth and flowering was hastened, but the ultimate seedstalk height and plant size was reduced. The number of umbels produced was greater at the higher temperatures, but their quality, as expressed in the number of umbellets per umbel and number of flowers per umbellet, was better at the lower temperatures. At 14°C the ratio of hermaphroditic to male flowers was in favor of the hermaphroditic flowers than at the higher temperature. Fertility of the male flowers was distinctly lower when grown at higher temperatures and that of the hermaphrodite flowers was not significantly affected.

Seedstalk height of carrots was reduced as the post-vernalization temperature increased from 15/20°C to 27/32°C (night/day) with no significant effect on flowering. Seedstalk height of 'Royal Chantenay' carrot was most affected by high temperatures and 'Scarlet Nantes' was the least affected while 'Denever 126' had seedstalks of intermediate height (Hiller and Kelly, 1979). They also reported that carrots grown at 27/32°C during the initial 6 weeks following vernalization and then transferred to the optimum 15/21°C grew no taller than plants held at 27/32°C.

Seed Priming

Seed priming is defined as the imbibition of seeds in an aerated osmotic solution at a concentration and temperature that allows the seeds to imbibe enough water to go through the first stages of germination but which prevents protrusion of the radicle through the seed coat (Heydecker *et al.*, 1975). Primed seeds can then be dried back to their original moisture content (Heydecker and Gibbins, 1978).

The purposes of seed priming generally include the following: (1) reduction of the time from sowing to seedling emergence, (2) decrease the spread of emergence in any given seed population, and (3) the ability of seeds to emerge under conditions of environmental stress such as high or low temperature (Guedes and Cantliffe, 1980; Heydecker, 1975; Heydecker and Coolbear, 1977; Simmonds, 1980).

Physiology and Biochemistry of Seed Priming

In most of the species tested, seed priming has been reported to cause a marked increase in germination rate, total germination percentage and seedling uniformity at lower or higher than optimum temperatures (Bleak and Keller, 1970; Bussel and Gray, 1976; Cantliffe *et al.*, 1984; Guedes and Cantliffe, 1980; Heydecker *et al.*, 1974, 1975; Koehler, 1967; Sachs, 1977). According to Heydecker (1975) priming caused "slow" and "fast" germinating seeds of a single population to attain the same stage of germination readiness, a property of considerable importance in obtaining uniform seedling emergence.

Koehler (1967) was the first to investigate the biochemical changes in tomato seeds in response to priming. Seeds were primed in 1% K_3PO_4 + 1% KNO_3 for 6 days at 24°C. Protein content and RNA level had increased 140 and 88%, respectively, by the end of the treatment.

Primed seeds reached an unnatural peak of respiration within 30 hrs after the treatment was initiated. An increase in RNA synthesis was also observed by Khan (1977) who reported that, when imbibed, primed seeds had a more rapid rate of polyribosome formation than untreated seeds. Koehler (1967) concluded that a mobilization of resources which exceeded that of normal germination was taking place in response to the priming treatment, while Khan (1977) suggested that increased protein synthesis in primed seeds might have resulted from an increased capacity to synthesize messanger RNA (mRNA) and/or from increased activation of existing ribosomal machinery. Coolbear and Grierson (1979) characterized the RNA accumulated during priming of tomato seeds to be a ribosomal RNA fraction. They found that the difference in RNA content between primed and untreated seeds was maintained during imbibition and into the lag phase of germination. However, they were unable to detect any abnormal accumulation of DNA, suggesting that cell division was not occurring in response to priming. Cantliffe et al. (1984) reported cell division and elongation after 10 hrs imbibition in primed lettuce seeds imbibed at 35°C. Neither process occurred in non-primed seeds, indicating that cell elongation and division were inhibited during high temperature imbibition in non-primed lettuce seeds. They concluded that seed priming appears to lead to an irreversible initiation of cell elongation, thus overcoming thermodormancy in lettuce. They also found that respiratory rates were higher in primed and non-primed lettuce seeds when imbibed at 35°C, compared to those imbibed at 25°C, although radicle protrusion did not occur in non-primed seeds, which were imbibed at 35°C. This finding suggests the exclusion of respiration as a factor causing thermodormancy or altered by thermodormancy on seed priming.

Malnassy (1977) examined the isoenzyme differences between treated and untreated seeds. They noted that the enzymatic changes that occurred during the treatment period were the same as those that occurred during the early stages of germination. Osmotic treatment of lettuce seeds enhanced the activity of certain enzymes, such as esterase and acid phosphatase (Tao and Khan, 1977).

Priming Solution (Osmoticum)

Osmotic sources used in priming are usually either salts such as potassium nitrate (KNO_3), monobasic or tribasic potassium phosphate (K_2HPO_4, K_3PO_4) or inert osmotica like polyethylene glycol (PEG) (Heydecker and Coolbear, 1977).

Ions from a salt solution can enter the cell with water, without slowing water uptake by the seed (Cantliffe et al., 1984). Polyethylene glycol (PEG) molecules are too large to enter the cell, allowing water only to enter the seeds, but the osmotic potential of the solution reduces the availability of water for uptake by the seed (Heydecker, 1973). Michel and Kaufmann (1973) considered PEG 6000 (molecular weight=6000) as more effective than PEG of lower molecular weights because it does not enter plant cells. However, the high viscosity of the PEG polymers with higher molecular weight (>4000) could detrimentally affect oxygen uptake by the seed (Heydecker, 1977).

Ells (1963) found that soaking tomato seeds in 1.5% K_3PO_4 plus 1% KNO_3 for 6 days improved tomato seed emergence at lower than optimum soil temperatures. Koehler (1967) reported earlier and more rapid germination of tomato seeds treated with 1.5% K_3PO_4 plus 1.5% KNO_3 in an aerated system. Tribasic potassium phosphate (K_3PO_4) at 1% solution was considered as standard solution for lettuce seed priming by Cantliffe (1980) and Cantliffe et al. (1984).

Some salts at certain concentrations, were reported to cause toxicity to seeds. Poor germination was reported when NaCl was used as soak solution for tomato, alfalfa and lettuce seeds (Mayer and Poljakoff-Mayber, 1975), and $CaCl_2$ for peas (Heydecker, 1967). Priming agents like KNO_3 and NaCl effectively caused earliness and synchrony of germination in many vegetable seeds (unspecified species), but the final percentage germination was either not affected or reduced with these salts (Aker and Brede, 1986). Bussell and Gray (1976) found that salt-primed tomato seeds germinated more rapidly than PEG-primed seeds at 8 or 10°C, but there was no difference between treatments at 15°C. O'Sullivan and Bouw (1984) reported that low temperature germination of pepper was accelerated by both salt and PEG priming at 20°C, but seeds primed in a solution of KNO_3 + K_3PO_4 had a faster rate of germination than PEG-primed seeds. Salter and Darby (1976) reported no difference between PEG and salt solutions in accelerating germination of celery.

The major advantage of PEG is that it does not have any adverse effect on seeds. Polyethylene glycol is considered as chemically inert material (Heydecker, 1974; Heydecker et al., 1974; Michel and

Kaufmann, 1973). Although, Reid et al. (1978) reported that PEG may contain phosphorus in concentrations as high as those found in soils.

Brussel sprouts had higher emergence and earlier yield from primed seeds compared to untreated seeds planted at low soil temperatures (Khan et al., 1981). Similarly, broccoli germination was increased by priming in -15 bars PEG 6000 at 20°C (Hegarty, 1977).

Szafirowska et al. (1981) reported that priming carrot seed in -8.6 bar PEG solution for 6 days at 15°C improved the emergence time and seeding establishment in cold soils, as well as the total root yield compared to the untreated seed. Khan et al. (1981) primed cabbage seeds in 30% PEG solution with 0.2% thiram at 15°C for 6 days. Although final emergence in cold soils was high for both primed and untreated seeds, primed seeds emerged 3 days earlier than untreated seeds. An increase in plant or head fresh weight of 28 to 50% between 50 to 120 days after planting was reported for primed treatments compared to controls. Although priming increased cabbage seedling emergence to sub-optimal soil temperatures of 8 to 15°C, the effect was lost when soil temperatures increased above 15°C (Khan et al., 1979).

Priming carrots, celery, leek and onion seeds in solutions of PEG 6000, glycerol and potassium diphosphate (KH_2PO_4) increased the rates of seed germination and seedling emergence compared to untreated controls. Glycerol-treated seeds germinated and emerged more slowly than did PEG- and KH_2PO_4-treated seeds. Potassium diphosphate treatment tended to reduce percentage germination and emergence, most markedly in leek and one cultivar of celery (Brocklehurst and Dearman, 1984). They concluded that PEG treatment gives the most consistently beneficial effects for the range of species they tested.

Temperature and Duration of Priming

Factors such as temperature and duration of soak have proved to be important as well as the type of the osmotic solution (Ells, 1963; Darby and Salter, 1976b; Cantliffe et al., 1978). Radicle emergence during priming can be slowed by priming seeds at temperatures below the optimum range for germination of the species. Koehler (1967) observed that maximum germination for soaked and redried tomato seed occurred after either a soak for 7 days at 24°C or for 28 days at 10°C. Ells (1963) reported that pretreatment with water alone or with a 1% KNO_3 + 1% K_3PO_4 solution for 6 days at 10°C was equivalent to soaking tomato seeds in water for 2 days at 24°C. Kirkwood (1970) reported that when imbibed pepper seeds were maintained for a number of days at temperatures too low to permit radicle protrusion, they germinated faster, upon transfer to a favorable temperature for germination, than seeds not treated at low temperatures.

There are some indications that pretreatment at favorable temperatures for germination facilitates subsequent germination at sub-optimal temperatures (Heydecker et al., 1975). Sachs (1977) reported a high germination percentage for watermelon seed at sub-optimal soil temperatures by priming the seeds for various periods of time at temperatures of 30 to 35°C.

The optimum duration of soak is dependent on the species, soaking temperature and the type of priming solution (Hegarty, 1970;

Heydecker, 1974; Heydecker and Hardy, 1975). Generally, soaks for longer periods at lower temperatures have an equivalent effect to shorter soaks at temperatures close to the germination optimum for the species.

Growth Regulators in Priming

A limited amount of work has been reported on the incorporation of various growth regulators in the priming solution. Brocklehurst *et al*. (1982) demonstrated that the inclusion of GA4/7 and ethephon in a PEG solution enhanced the rate and total emergence of celery over priming in PEG alone or over seeds given GA-ethephon soaks before or after priming in PEG alone. While PEG treatment extended the upper temperature limit for dark germination of celery from 18 to 21.4°C, the inclusion of GA and ethephon extended it to 24°C. Addition of benzyl adenine (BA) to the PEG solution enhanced the effect of PEG treatment on the rate of germination of celery seed at 20, 25, and 30°C, but the addition of $GA_{4/7}$ had no effect (Nakamura *et al*., 1982). Khan *et al*. (1981) reported that inclusion of $GA_{4/7}$, kinetin and ethephon in the priming solution prevented the secondary dormancy in lettuce. Cantliffe and Watkins (1983) found that incorporation of 100 ppm $GA_{4/7}$ enhanced the effects of priming pepper seed in a PEG solution.

Species, Cultivar and Seed Lot Responses to Priming

The advantages of priming in advancing germination time and extending germination range have been variable when applied to different species, cultivars and seed lots. Perkins-Veazie and Cantliffe (1984) emphasized the need for high quality seed lots to obtain the full advantages of priming. They reported that aged lettuce seed responded poorly to priming in relation to enhancing germination at high temperatures. Brocklehurst and Dearman (1983a) found that the mean days to germination (MDG) for all seed lots of all cultivars tested of carrot, celery and onion was reduced by priming in PEG for 2 weeks at 15°C. The interaction between priming treatments and cultivars and between priming and seed lots within cultivars were highly significant for each species. The largest reductions in MDG due to priming were obtained in the poorest seed lots, and the spread of germination was reduced by priming in all cultivars. Priming in PEG improved the percentage emergence in poorer seed lots of carrot and celery but not onion (Brocklehurst and Dearman, 1983b).

The Effects of Storage on Viability of Primed Seeds

In most of the species studied, primed seeds have been reported to store as well as non-primed seeds. Cantliffe et al. (1977) reported that germination of cabbage and pepper seeds 4.5 months after treatment was as high as that of freshly treated seeds. Similar results were reported for seeds of pepper (Yaklich and Orzoleck, 1977) and watermelon (Sachs, 1977). In some cases, however, the advantages obtained in priming were lost with time. Celery seeds treated with PEG deteriorated very rapidly with storage time (Thomas et al., 1978). Prolonged storage of primed tomato 'FloraDade' seeds resulted in reduced germination rates and total percentage germination particularly at supra-optimal temperatures (35°C) (Odell, 1986).

Thompson and Horn (1944) reported that the longevity of primed seeds in storage was more dependent on the storage conditions than on the priming treatment itself. Ten lettuce seed strains treated with thiourea or water after 2 months storage germinated as well as at the beginning of the storage period when stored at 10 to 12°C. However, germination declined from 6.6 to 10.8%, respectively, for thiourea- and water-treated seeds when they were stored for the same period of time at 20 to 30°C. In tomato, the reduction in time to 50% germination due to priming in PEG or KNO_3 was retained for at least 18 months at 15 and 25°C storage temperatures. However, at 30°C, primed seeds were more susceptible to loss of viability and vigor than unprimed seeds, particularly for KNO_3-primed seeds (Alvarado and Bradford, 1986).

Summary

From the preceding review, it appears that poor seed quality in carrot, is caused by a combination of many factors. Among these factors are flowering morphology of the seed plant, environment during seed development and maturation, level of pollination, seed pests and diseases and cultural practices.

Flowering morphology of carrot seed plants and its effect on seed maturity is believed to be the most troublesome among these factors. Any attempt to improve seed quality in carrot should confront the manipulation of plant morphology on seed quality. Growth retardants are known to cause retardation in many plants, with no adverse effects on flowering under inducive conditions. The objective of the first section of this work was to investigate the use of growth retardants, as chemical pruning agents, to modify the fall flowering morphology of carrot, and to define the effect of seed stalk development through chemical or hand pruning on seed yield and seed quality in carrots.

Environmental conditions experienced by the mother plants have major effects on seed yield and seed vigor. Among environmental factors, temperature has the dominant effect on seed yield and quality. During the last decade, most carrot seed producing companies shifted their seed production area from Idaho to the Cascade Mountains in Oregon. The latter area has a cooler environment compared to Idaho and Southern California. This move resulted in an increase in seed yield and improvement of seed quality. The objective of the second part of this study was to investigate whether seed crop growing temperature has any effect on seed yield and vigor in carrot.

The performance of many vegetable and agronomic crop seeds can be improved by seed priming. Although seed priming does not represent an alternative to production of high quality seed, it can be used to enhance germination under unfavorable conditions. Seed lot interaction with priming treatment is a major problem in carrots. The objective of the last section of this work was to study the effect of growth regulators addition to priming solution on the performance of different carrot seed lots at different temperatures.

CHAPTER III
CONTROL OF CHEMICAL REGULATORS ON FLOWERING, SEEDSTALK DEVELOPMENT, SEED YIELD AND SEED QUALITY OF CARROTS (*Daucus carrota* L.)

Introduction

The influence of seed position on the mother plant on seed size and quality has been reported in many plant species: barley (Austin, 1979), wheat (Strona, 1966; Bremner, 1972), lettuce (Soffer and Smith, 1974) and celery (Thomas et al., 1979). The effect of seed position is even more profound in carrots, due to the flowering morphology of the plant (Chapter II). Because of the complexity of flowering in carrot, seed maturation does not occur at one time on each plant, but begins progressively later the higher the umbel order.

At maturity, the primary umbels on each plant have the largest seeds, and the tertiary umbels have the smallest (Malik and Kanwar, 1969; Gray and Steckel, 1980; Jacobsohn and Globerson, 1980). Seeds produced on the primary umbels generally have the highest germination percentage, followed by seeds from the secondaries, which in turn generally germinate better than seeds from the tertiary umbels (Borthwick, 1931a; Hawthorn et al., 1962; Nath and Valvi, 1969).

Harvest time represents a major challenge to carrot seed growers and seed companies, because of the complicated flowering pattern of the plants. Seed harvest must be delayed sufficiently to obtain mature seeds with higher and vigorous germination, however, it should be made early enough to avoid seed loss from the primary umbels and the lower secondaries. Commercially, seed growers make a single harvest when the whole field is judged to be predominately mature. The harvested seed, therefore, comprises seed at different stages of maturity (Gray, 1983).

Since high quality seeds are produced from the lower umbel orders (primary and secondary orders), it has been suggested that effort should be made to reduce the proportion of yield contributed by the higher orders (tertiaries and higher) (Jacobsohn and Globerson, 1980; Gray, 1981).

Early workers (Hagije, 1954; Miyagi, 1956; Krarup et al., 1976) have shown that removing the secondary umbels during early plant growth increased seed size and improved seed viability. However, even if this technique was to reduce root variability, it would probably be economically infeasible, as seed yields are greatly reduced and the nature of labor is intensive (Gray, 1983).

Another approach suggested for improving carrot seed quality without loss of seed yield was to modify the morphology of the flowering plants, by decreasing plant spacing (Gray, 1981, 1983). At high plant densities, the development of lateral branches is suppressed and the majority of seeds comes from the primary umbels. However, increasing plant density has resulted in an increase in the spread of flowering of the primary umbels, which caused an increase in the variation of seedling weight from mature seeds (Gray and Steckel, 1985).

An alternative method for modifying plant morphology would be the application of chemical regulators to the seed crops. Application of

Chlormequat (CCC) to lettuce plants reduced seed stalk height and improved seed germination (Thomas, 1968). Similarly, seedstalk height in brussel sprouts was reduced, while seed yield and percentage germination were increased by the application of Daminozide at 4000 ppm (Thomas and Toole, 1980).

The objective of this study was to investigate whether application of certain chemical regulators could modify flowering morphology in carrots, and thereby improve seed maturation uniformity and seed quality.

Materials and Methods

Carrot (*Daucas carota*) cultivar 'Hicolor-9' (Asgrow Seed Co.) roots (stecklings) were produced from seed on raised beds at the Horticultural Unit, at the University of Florida, on Pomona fine sand. At maturity, roots were harvested by hand. Medium-size, uniform roots were selected. Tops were cut about 6 cm above the crown, roots were cut to approximately 12 cm and rinsed to remove adhering field soil. The roots were then dipped in 0.2% Thiram solution, placed in perforated plastic bags with vermiculite to prevent desiccation, and stored for about 8 weeks at 5°C.

After cold storage, roots were potted in 2:1:1 peat:vermiculite:perlite mixture in the greenhouse. Spacing between plants within the bench was 30 cm within row and 45 cm between rows. The plants were fertilized weekly with 20:9:17 (N:P:K). Fertilizers were applied through a drip system at the rate of 1 tablespoon/gallon, with each plant receiving approximately 200 mL. After flowering, the main seed stalks were tied to bamboo stakes for support. To ensure maximum pollination, house flies were raised and introduced in the greenhouse after screening the bench with Saran Screen. The rearing method for the house fly (Musca domestica) described by Morgan (1981) was followed.

The experiments in this study were conducted during Fall 1983, Summer 1984, and Fall 1984. Planting and harvest dates for each experiment are shown in Appendix Table A-1. Maximum and minimum temperatures in the greenhouse during fall 1983, summer 1984, and fall 1984 are shown in Appendix Table A-2.

Experimental Procedures

Experiment I. This experiment was conducted in the fall of 1983. Five chemical regulators were used in this experiment at the following concentrations: Gibberellic acid (GA_3) (Amdal Co.), 1000 ppm; Ancymidol (A-Rest) (Elanco), 100 and 250 ppm; Chlormequat (CCC) (American Cyanamid Co.), 2000 and 5000 ppm; Daminozide (B-9) (Uniroyal), 2000 and 5000 ppm; and Phosphon-D (Carolina Bio. Supply Co.), 250 and 500 ppm. Aqueous solutions of GA_3, Daminozide and Phosphon-D were applied with a pipette (1 ml/plant) directly on the apical meristem, 2 weeks after potting twice weekly for 4 weeks. Ancymidol and Chlormequat were applied as soil drenches, 20 and 200 ml/pot, respectively, twice weekly for 2 weeks.

Experiment II. Experiment I was replicated during the summer of 1984. In this experiment, GA_3 treatment was excluded. Other treatments were maintained as described in Experiment I.

Experiment III. In the fall of 1984, only Ancymidol at 25, 50 or 100 ppm and Daminozide at 1000, 2000, 4000 or 8000 ppm were used. Both chemicals were applied to the apical meristem, 2 weeks after planting, twice weekly for either 2 weeks for Ancymidol or 4 weeks for Daminozide. Pruning of the tertiary umbels was introduced as another treatment in this experiment.

Data Collection

The number of days to primary umbel anthesis was used as indicator for flowering time. Each plant was tagged on the date of anthesis of the first flower on the primary umbel. Seeds were harvested when the seeds on the tertiary umbels reached maturity. All plants were harvested on the same date regardless of their maturity time. Seed stalk height was measured and number of umbels per each order and total number of umbels per plant were recorded.

Seed threshing and cleaning were done manually. Seed yield per umbel order and total yield per plant were expressed as grams of clean seeds. The contribution of each umbel order to the total seed yield per plant was calculated using the following formula

$$\text{\% Order contribution} = \frac{\text{seed yield per order (gram)}}{\text{total seed yield per plant (gm)}} \text{ X } 100.$$

The harvested seeds from each umbel order were kept separately and stored at 10°C and 25% R.H.

Seed Quality Evaluation

Total percentage germination and mean days to germination (MDG) were determined using standard germination test and accelerated aging test. For accelerated aging test, at least 100 seeds in four replicates from each order were placed on wire mesh screens in plastic containers (11 x 11 x 3.5 cm) above 100 ml water. The containers were sealed and incubated at 41°C for 4 days. Relative humidity in the containers was nearly 100%. After 4 days, the seeds were removed and dried at 15°C and 25% R.H., for 7 days.

Seeds were germinated at 25°C on moistened Whatman No. 1 and No. 3 filter papers in 9-cm Petri dishes. Germination counts were taken at 24-hour intervals for 14 days. Four replicates of 25 seeds per Petri dish were made. Seeds with visible radicles were counted as germinated.

Mean days to germination (MDG) were calculated by the formula used by Gerson and Honma (1978)

$$\text{MDG} = \frac{\text{(Days to germination)(Number of seeds germinated)}}{\text{Total number of seeds germinated}} .$$

Seedling vigor was determined by measuring radicle length, hypocotyl length, fresh weight and dry weight. These measurements were obtained by placing four replicates of 10 seeds on moist germination papers. The papers were rolled up with a wax paper backing and placed in incubators at 25°C. Growth measurements were made after 14 days.

Statistical Analyses

The experimental design used in the three experiments was a completely randomized design, with three replicates in Experiment I and six replicates in Experiments II and III. All data were subjected to analysis of variance and significant differences between means determined by Duncan's multiple range test or least significant difference test. Orthogonal contrasts were used when applicable.

Results

Number of Days to Flowering, Seed Stalk Height and Number of Umbels

Experiment I. Seed stalk initiation and elongation were observed earlier in plants which were treated with GA_3. However, anthesis of the primary umbel flowers was not significantly earlier than other treatments (Table 3-1). Generally, number of days to primary umbel anthesis was unaffected by any treatment.

Compared to the control seed stalk height was increased by GA_3 and reduced by Ancymidol, Daminozide, Chlormequat and Phosphon-D at both concentrations. Total number of umbels per plant was reduced by both concentrations of Ancymidol and Daminozide and the lower concentration of Chlormequat (i.e., 2000 ppm) and Phosphon-D (i.e., 250 ppm). Gibberellic acid (GA_3) and the higher concentrations of Chlormequat (5000 ppm) and Phosphon-D (500 ppm) had no effect on total number of umbels per plant (Table 3-1).

The reduction in the total number of umbels by Ancymidol was due to the decrease in the number of secondary umbels by both

Table 3-1. Effects of various chemical regulators on number of days to primary umbel anthesis, seedstalk height, number of umbels per order and total number of umbels per plant for Experiment I, fall 1983.

Treatment	No. days to anthesis	Seedstalk height	Number of umbels per order 2°	3°	4°	Total number of umbels per plant
— ppm —		—— cm ——				
Control	76	71	8	16	9	34
GA_3 1000	64	126	7	16	9	33
Ancymidol 100	75	20	4	9	5	19
Ancymidol 250	74	24	4	5	4	14
Daminozide 2000	77	69	5	6	1	13
Daminozide 5000	77	47	5	6	2	14
Chlormequat 2000	64	45	7	9	5	22
Chlormequat 5000	69	44	6	16	9	32
Phosphon-D 250	74	44	6	9	4	20
Phosphon-D 500	74	34	7	16	9	33
Contrasts						
GA_3 vs Others	NS[z]	**	NS	NS	NS	NS
Control vs. Ancymidol, Daminozide	NS	*	**	**	**	**
Daminozide vs. Ancymidol	NS	**	NS	NS	NS	NS
Daminozide 2000 vs. 5000	NS	*	*	NS	NS	NS
Ancymidol vs. Chlormequat	NS	NS	NS	NS	NS	NS

Table 3-1—continued.

Treatment	No. days to anthesis	Seedstalk height	Number of umbels per order			Total number of umbels per plant
			2°	3°	4°	
— ppm —		— cm —				
Ancymidol 100 vs. 250	NS	NS	NS	NS	NS	NS
Chlormequat 2000 vs. 5000	NS	NS	NS	NS	NS	*
Chlormequat vs. Phosphon-D	NS	NS	NS	NS	NS	NS
Phosphon-D 250 vs. 500	NS	NS	NS	NS	*	*

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[z] F values significant at 0.01 level (**), 0.05 level (*), or not significant (NS).

concentrations, accompanied by a decrease in the number of tertiary umbels caused by the higher concentration of Ancymidol. The number of quaternary umbels was not affected by Ancymidol application (Table 3-1).

Daminozide had no effect on the number of umbels on the secondary order, however, it reduced the number of umbels on both tertiary and quaternary orders. Gibberellic acid, Chlormequat and Phosphon-D had no effect on the number of umbels on any of the three orders when taken individually. Although, Chlormequat and Phosphon-D, at their lower concentrations, reduced the total number of umbels per plant (Table 3-1).

Experiment II. The effect of chemical regulator applications on number of days to primary umbel anthesis, seedstalk height, and number of umbels is shown in Appendix Table A-3. Application of chemical regulators had no effect on number of days to primary umbel anthesis. All treatments significantly reduced seedstalk height compared with the control. The branching habit of the plants was generally the same among all of the treatments during the summer of 1984.

Experiment III. Based on the results of experiment I, only Ancymidol at 25, 50, and 100 ppm, and Daminozide at 1000, 2000, 4000 or 8000 ppm were used during the fall of 1984. Application of Ancymidol at 50 ppm resulted in a significant delay in primary umbel anthesis, when compared to the control, however, this delay was not significantly different when compared to the other two concentrations of Ancymidol (Table 3-2). Daminozide had no effect on number of days to primary umbel anthesis.

Table 3-2. Effects of Ancymidol, Daminozide and pruning of tertiary umbels on number of days to primary umbel anthesis, seedstalk height, number of umbels per order and total number of umbels per plant for Experiment II, fall 1984.

Treatment	No. days to anthesis	Seedstalk height	Number of umbels per order			Total number of umbels per plant
			2°	3°	4°	
— ppm —		— cm —				
Control	54	72	11	22	15	49
Ancymidol 25	57	21	5	14	10	29
Ancymidol 50	63	12	4	8	8	21
Ancymidol 100	59	20	4	8	5	19
Daminozide 1000	54	41	4	9	6	20
Daminozide 2000	62	34	6	14	9	30
Daminozide 4000	57	35	6	13	8	29
Daminozide 8000	61	25	7	17	16	41
Pruning	65	69	10	-	-	11
Contrast						
Pruning vs All	*[z]	**	**	NE	NE	**
Ancymidol vs control, Daminozide	NS	**	**	**	*	**
Control vs Daminozide	NS	**	**	**	**	**
Ancymidol 25 vs 50, 100	NS	NS	NS	*	NS	NS
Ancymidol 50 vs 100	NS	NS	NS	NS	NS	NS
Daminozide 1000 vs 2000, 4000, 8000	NS	NS	**	**	**	**

Table 3-2—continued.

Treatment	No. days to anthesis	Seedstalk height	Number of umbels per order 2°	3°	4°	Total number of umbels per plant
— ppm —		—— cm ——				
Contrast						
Daminozide 2000 vs 4000, 8000	NS	NS	NS	NS	NS	NS
Daminozide 4000 vs 8000	NS	NS	NS	NS	**	**

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[z] F values significant at 0.01 level (**), 0.05 level (*), not significant (NS), or non estimable (NE).

Similar to the results obtained in Experiments I and II, Ancymidol and Daminozide at all concentrations reduced seedstalk height. The reduction caused by Ancymidol was greater when contrasted against the control and Daminozide. Orthogonal contrast analysis revealed no significant differences between the different concentrations of either Ancymidol or Daminozide.

Ancymidol, at all concentrations, and Daminozide at 1000, 2000 and 4000 ppm, reduced the total number of umbels per plant. This reduction was equally distributed on the three orders (Table 3-2). Application of Daminozide at 8000 ppm reduced the number of umbels on the secondary order, however, it had no effect on the number of umbels on the tertiary and quaternary orders or the total number of umbels per plant.

Increasing Ancymidol concentration above 25 ppm significantly reduced the total number of umbels per plant and number of umbels on tertiary orders. However, increasing the concentration from 50 to 100 ppm had no effect on the total number of umbels or the number of umbels on any order. Daminozide was more effective on reducing actual umber numbers when applied at 1000 ppm compared to 2000, 4000 or 8000 ppm. Increasing Daminozide concentration above 2000 ppm had no effect on the total number of umbels or umbel numbers on any of the three orders. However, increasing the concentration above 4000 ppm resulted in the reversal of the chemical effect and led to an increase in the number of umbels on the quaternary orders and thus, total number of umbels per plant.

Table 3-3. Effects of various chemical regulators on seed yield of each umbel order and total seed yield per plant for Experiment II.

Treatment	Umbel order						Total seed yield
	1°	2°	1° and 2°	3°	4°	3° and 4°	
— ppm —	gm seed per umbel order						gm seed per plant
Control	1.6	6.7	8.3	3.2	0.8	4.0	12.3
GA_3 1000	1.8	7.8	9.6	4.1	0.4	4.5	14.1
Ancymidol 100	1.2	2.0	3.2	3.0	0.1	3.1	6.3
Ancymidol 250	1.5	2.0	3.5	1.5	0.0	1.5	5.0
Daminozide 2000	2.9	4.4	7.3	1.0	0.0	1.0	8.3
Daminozide 5000	2.6	5.0	7.6	1.5	0.2	1.7	9.3
Chlormequat 2000	1.4	7.3	8.7	4.7	0.3	5.0	13.7
Chlormequat 5000	1.6	7.8	9.4	8.3	0.4	8.7	18.1
Phosphon-D 250	2.0	6.8	8.8	4.8	0.1	4.9	13.7
Phosphon-D 500	1.6	7.7	9.3	5.4	0.2	5.6	14.9
Contrasts							
GA_3 vs Others	NS[z]	NS	NS	NS	NS	NS	NS
Control vs. Ancymidol, Daminozide	NS	**	*	NS	**	NS	**
Daminozide vs. Ancymidol	NS	*	**	NS	NS	NS	NS
Daminozide 2000 vs. 5000	NS	NS	NS	NS	NS	NS	NS
Ancymidol vs. Chlormequat	NS	**	**	**	NS	**	**

Table 3-3—continued.

Treatment	Umbel order 1°	2°	1° and 2°	3°	4°	3° and 4°	Total seed yield
— ppm —	gm seed per umbel order						gm seed per plant
Ancymidol 100 vs. 250	NS	NS	NS	NS	NS	NS	NS
Chlormequat 2000 vs. 5000	NS	NS	NS	*	NS	*	NS
Chlormequat vs. Phosphon-D	NS	NS	NS	NS	NS	NS	NS
Phosphon-D 250 vs. 500	NS	NS	NS	NS	NS	NS	NS

[z] F values significant at 0.01 level (**), 0.05 level (*), or not significant (NS).

Hand pruning of the tertiary umbels obviously reduced total number of umbels per plant. But, application of Ancymidol at 50 or 100 ppm or Daminozide at 1000 ppm was as effective as pruning in reducing number of umbels per plant.

Seed Yield

Experiment I. Ancymidol at both concentrations reduced total seed yield per plant (Table 3-3). This reduction was restricted to the secondary and quaternary orders only. Daminozide had no significant effect on total seed yield, although there was a tendency toward reducing it. Total seed yields from plants treated with Chlormequat or Phosphon-D were the same as the control.

Chemical regulators had no effect on the amount of seed produced by the primary order. However, Daminozide, at both concentrations substantially although not significantly increased seed yield. Seed yield from the secondary umbel order and from both primary and secondary orders was reduced with Ancymidol application. Chlormequat at 5000 ppm was the only treatment that affected tertiary umbel yield and the seed yield from the tertiary and quaternary orders combined. Daminozide at 2000 ppm and Ancymidol at both concentrations reduced seed yield from the quaternary umbel, although their effects were not different from the effects of other chemical regulators.

Experiment II. Only Daminozide at 2000 ppm and Phosphon-D at 500 ppm reduced total seed yield per plant, primary order and secondary order seed yield (Appendix Table A-4). Both chemicals, at the mentioned concentrations, had no effect on seed yield of the tertiary and quaternary orders. Other chemicals showed no effect on total seed yield or seed yield of any of the four umbel orders when compared to the control.

Experiment III. During the fall of 1984, application of Ancymidol at all concentrations reduced the total seed yield per plant and secondary order seed yield (Table 3-4). Primary order seed yield was reduced by Ancymidol at 25 and 100 ppm, while that of the tertiary order was reduced by the two lowest concentrations (i.e., 25 and 50 ppm). Orthogonal contrast comparisons revealed no differences among the three concentrations of Ancymidol used.

Primary, secondary and quaternary order seed yield was unaffected by Daminozide at all concentrations. However, all concentrations of Daminozide reduced the amount of seed obtained from the tertiary order (Table 3-4). Total seed yield per plant was reduced only by the highest concentration (i.e., 8000 ppm). Application of Daminozide at 1000 ppm resulted in higher seed yield from the primary order, tertiary and quaternary order, compared to 2000, 4000 and 8000 ppm, but it had no effect on the secondary order yield and total seed yield per plant (orthogonal contrast). There was no difference between 2000, and 4000 and 8000 ppm; however, increasing the concentration from 4000 ppm to 8000 ppm caused an increase in the quaternary order seed yield.

Hand pruning of the tertiary umbels reduced the total seed yield when compared to the untreated control. However, the difference

Table 3-4. Effects of Ancymidol, Daminozide and pruning of tertiary umbels on seed yield per each umbel order and total seed yield per plant for Experiment III, fall 1984.

Treatment	Umbel order				Total seed yield
	1°	2°	3°	4°	
— ppm —	—— gm seed per umbel order ——				gm seed per plant
Control	4.3	10.6	6.5	0.3	21.7
Ancymidol 25	1.8	5.9	3.2	0.9	11.9
Ancymidol 50	2.6	4.4	2.2	1.0	10.3
Ancymidol 100	1.1	4.2	4.0	0.6	8.6
Daminozide 1000	4.9	7.9	3.7	0.2	16.7
Daminozide 2000	2.7	8.6	2.0	0.5	13.8
Daminozide 4000	4.5	8.9	2.5	0.2	16.1
Daminozide 8000	3.2	6.9	2.3	0.6	12.9
Pruning	4.1	11.1	-	-	15.1
Contrasts					
Pruning vs All	NS[z]	*	NE	NE	NS
Ancymidol vs control, Daminozide	**	**	NS	NS	**
Control vs Daminozide	NS	NS	**	NS	**
Ancymidol 25 vs 50, 100	NS	NS	NS	NS	NS
Ancymidol 50 vs 100	NS	NS	NS	NS	NS
Daminozide 1000 vs 2000, 4000, 8000	*	NS	**	**	NS
Daminozide 2000 vs 4000, 8000	NS	NS	NS	NS	NS
Daminozide 4000 vs 8000	NS	NS	NS	**	NS

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[z] F values significant at 0.01 level (**), 0.05 level (*), not significant (NS), or non estimable (NE).

between pruning and Ancymidol or Daminozide was not significant. Primary and secondary orders seed yield were unaffected by pruning (Table 3-4). When contrasted against all other treatments, hand pruning had no effect on primary order seed yield, and total seed yield and significantly increased secondary order seed yield.

Contribution of Umbel Orders to Seed Yield

Experiment I. The effect of chemical regulators on the contribution of different umbel orders to the final seed yield during the fall of 1983 is shown in Table 3-5. Contribution of the primary order and the secondary order was not significantly affected by chemical regulators, although, Ancymidol and Daminozide had a tendency of increasing the contribution of the primary order to seed yield, while Ancymidol had a tendency of reducing the contribution of the secondary order.

Ancymidol at 100 ppm and Chlormequat at 5000 ppm, significantly reduced the contribution of the primary and secondary order toward the final seed yield, when compared to Daminozide. However, all treatments had not affected the contribution of primary and secondary orders, when compared to the control (Table 3-5).

The contribution of the tertiary order and that of the tertiary and quaternary orders, were affected by chemical regulators, in the same pattern of the primary and secondary orders contribution. Application of Daminozide at 2000 ppm and Ancymidol at 250 ppm reduced the percentage of seed contributed by the quaternary order (Table 3-5).

Table 3-5. Effects of various chemical regulators on the contribution (%) of different umbel orders to the final seed yield, Experiment I, fall 1983.

	Umbel order					
Treatment	1°	2°	1° and 2°	3°	4°	3° and 4°
— ppm —	% seed per umbel order					
Control	13.1	55.7	68.7	24.8	6.4	31.3
GA_3 1000	12.4	55.3	67.7	28.8	3.4	32.3
Ancymidol 100	20.4	32.9	53.2	45.4	1.4	46.8
Ancymidol 250	27.4	36.9	64.2	35.2	0.6	35.8
Daminozide 2000	36.6	54.9	88.5	11.5	0.0	11.5
Daminozide 5000	24.0	58.2	82.2	16.3	1.5	17.8
Chlormequat 2000	10.0	53.4	64.6	34.5	1.1	34.5
Chlormequat 5000	10.0	42.3	52.3	44.9	2.8	47.7
Phosphon-D 250	21.0	46.4	67.4	30.7	0.8	32.6
Phosphon-D 500	14.7	48.9	63.6	34.6	1.7	36.4
Contrasts						
GA_3 vs Others	NS^z	NS	NS	NS	NS	NS
Control vs. Ancymidol, Daminozide	NS	NS	NS	NS	**	NS
Daminozide vs. Ancymidol	NS	**	**	*	NS	**
Daminozide 2000 vs. 5000	NS	NS	NS	NS	NS	NS
Ancymidol vs. Chlormequat	NS	NS	NS	NS	NS	NS

Table 3-5—continued.

Treatment	Umbel order					
	1°	2°	1° and 2°	3°	4°	3° and 4°
— ppm —	% seed per umbel order					
Ancymidol 100 vs. 250	NS	NS	NS	NS	NS	NS
Chlormequat 2000 vs. 5000	NS	NS	NS	NS	NS	NS
Chlormequat vs. Phosphon-D	NS	NS	NS	NS	NS	NS
Phosphon-D 250 vs. 500	NS	NS	NS	NS	NS	NS

[z] F values significant at 0.01 level (**), 0.05 level (*), or not significant (NS).

Experiment II. All treatments had no effect on the contribution of any of the umbel orders, when compared to the control during the summer 1984 experiment (Appendix Table A-5). Application of Ancymidol at 100 or 250 ppm reduced the contribution of the secondary order, the primary and secondary orders combined, and increased the contribution of the tertiary and quaternary order combined compared to Phosphon-D at 500 ppm. Application of Phosphon-D at 500 also reduced the contribution of the tertiary order and the contribution of the quaternary order compared to the low and high concentration of Ancymidol, respectively (i.e., 100 and 250 ppm, respectively).

Experiment III. Hand pruning of the tertiary umbels had no effect on the contribution of the primary order to the final yield, but it resulted in a significant increase in the percentage of the seed contributed by the secondary order to the final seed yield (Table 3-6). Application of Ancymidol led to a significant decrease in the contribution of the primary order, the contribution of the secondary order and the contribution of the primary and secondary order, and significantly increased the contribution of the tertiary order, quaternary order and the tertiary and quaternary orders, when compared to the control and Daminozide. Increasing the concentration of Ancymidol from 25 ppm to 100 ppm had no effect on the contribution of any of the orders to seed yield.

Application of Daminozide reduced the contribution of the tertiary order to seed yield, when compared to the control. However, it had no effect on other orders' percentage contributions (Table 3-6). Similar to Ancymidol, the increase in the contribution of

Table 3-6. Effects of Ancymidol, Daminozide and hand pruning of tertiary umbels on the contribution (%) of different umbel orders to the final seed yield, Experiment III, fall 1984.

Treatment	Umbel order					
	1°	2°	1° and 2°	3°	4°	3° and 4°
— ppm —	% seed per umbel order					
Control	10.2	47.1	67.4	26.6	10.0	37.6
Ancymidol 25	16.0	49.0	65.1	28.7	6.3	34.9
Ancymidol 50	20.4	37.1	57.6	29.6	11.9	41.5
Ancymidol 100	12.2	45.4	57.5	37.2	5.2	42.4
Daminozide 1000	30.9	47.5	78.3	20.8	0.8	21.6
Daminozide 2000	20.3	61.2	81.5	15.0	3.4	18.5
Daminozide 4000	28.6	55.4	84.0	15.1	0.9	16.0
Daminozide 8000	23.6	53.9	77.5	16.5	6.0	22.7
Pruning	26.8	73.0	99.8	-	-	-
Contrasts						
Pruning vs All	NS^z	**	**	NE	NE	NE
Ancymidol vs control, Daminozide	**	*	**	**	*	**
Control vs Daminozide	NS	NS	NS	*	NS	NS
Ancymidol 25 vs 50, 100	NS	NS	NS	NS	NS	NS
Ancymidol 50 vs 100	NS	NS	NS	NS	NS	NS
Daminozide 1000 vs 2000, 4000 8000	NS	NS	NS	NS	NS	NS

Table 3-6—continued.

Treatment	Umbel order 1°	2°	1° and 2°	3°	4°	3° and 4°
— ppm —	% seed per umbel order					
Contrasts						
Daminozide 2000 vs 4000, 8000	NS	NS	NS	NS	NS	NS
Daminozide 4000 vs 8000	NS	NS	NS	NS	NS	NS

[z] F values significant at 0.01 level (**), 0.05 level (*), not significant (NS), or non estimable (NE).

Daminozide had no significant effect on seed distribution between different orders.

1000-Seed Weights

The effect of treatment and umbel order on seed size was determined through determining the 1000-seed weight.

Experiment I. There was an interaction ($P = 0.05$) between growth regulators and umbel order. Weight of seed developed on primary umbels was reduced from the control by Phosphon-D at 500 ppm, and increased by the high concentration of Daminozide, and the low concentration of Ancymidol and Chlormequat. Weight of secondary umbel seeds was reduced by the high concentration of Phosphon-D, and increased by Ancymidol at both concentrations, the low concentration of Chlormequat and Phosphon-D. Gibberellic acid and Phosphon-D at 500 ppm had no effect on tertiary umbel seed weight, however, all other treatments significantly increased the weight of tertiary umbel seeds (Table 3.7).

Experiment III. Similar to Experiment I, there was an umbel order and chemical regulator treatment interaction on 1000 seed weight. Primary umbel order seed weight was reduced by Ancymidol at 50 ppm and Daminozide at 1000 ppm, and increased by Ancymidol at 25, Daminozide at 2000 and 8000 ppm and hand pruning of the tertiary order. Seed weight of the secondary and tertiary orders was reduced by all treatments.

Table 3-7. Effects of various chemical regulators and umbel orders on 1000-seed weight for Experiment I, fall 1983.

Treatment	Umbel order		
	1°	2°	3°
— ppm —	1000-seed weight (gm)		
Control	1.02	1.06	0.96
GA_3 1000	0.98	1.03	0.93
Ancymidol 100	1.17	1.16	1.07
Ancymidol 250	1.11	1.28	1.18
Daminozide 2000	0.90	1.14	1.27
Daminozide 5000	1.25	1.05	1.17
Chlormequat 2000	1.17	1.25	1.21
Chlormequat 5000	0.98	1.04	1.23
Phosphon-D 250	1.05	1.16	1.19
Phosphon-D 500	0.97	0.91	0.89

LSD (0.05) Treatment x umbel order = 0.09.

Table 3-8. Effects of Ancymidol, Daminozide and pruning of tertiary umbels and umbel orders on 1000-seed weight, Experiment III, fall 1984.

Treatment	Umbel order		
	1	2	3
— ppm —	1000-seed weight (gm)		
Control	0.96	1.11	1.46
Ancymidol 25	1.03	0.87	1.28
Ancymidol 50	0.77	0.90	1.12
Ancymidol 100	0.96	0.97	1.42
Daminozide 1000	0.82	0.82	1.17
Daminozide 2000	1.15	1.05	1.40
Daminozide 4000	0.97	0.87	0.94
Daminozide 8000	1.07	0.79	1.04
Pruning	1.04	0.96	-

LSD (0.05) Treatment x umbel order = 0.03.

Seed Germination

Because of an interaction between chemical treatments of the mother plant, umbel orders and seed aging, the complete data for total percentage germination and MDG for Experiment I are presented in Table 3-9. The germination of non aged primary order seeds was improved by GA_3, Daminozide at 5000 and Chlormequat at 2000 ppm, and unaffected by other treatments. Accelerated aging had no effect on the germination of primary umbel seeds obtained from control plants or those treatments with GA_3 or Phosphon-D at 500 ppm, but led to reduced germination of aged seeds from the remaining treatments.

Total germination of non aged secondary order seed was greater than aged seeds in all chemical regulator treatments (Table 3-9). Seed aging had no effect on the germination of secondary umbel seeds from untreated control plants. Three treatments, Ancymidol at 250 ppm and Chlormequat at 2000 and 5000 ppm had greater germination of non aged secondary umbel seeds, when compared to the control.

Application of chemical regulators to the mother plant had no effect on the germination percentage of non aged tertiary order seeds, compared to the control (Table 3-9). Germination of aged tertiary order seed was unaffected by Ancymidol at 100 ppm, Chlormequat at 5000 ppm and Phosphon-D at 250 ppm, and increased by all remaining treatments, compared to the control.

Germination of nonaged seeds from the primary order was delayed compared to the control by Ancymidol at 100 ppm and unaffected by the other treatments (Table 3-9). After 4 days of aging, primary order

Table 3-9. Effects of mother plant treatments, umbel orders and seed aging on total percentage germination and mean days to germination for Experiment I, fall 1983.

Treatment	Aging	Total percentage germination			Mean days to germination		
		1°	2°	3°	1°	2°	3°
— ppm —			%			days	
Control	–	68[z]	81	89	3.0[y]	3.6	3.7
	+	56	77	32	5.0	5.5	6.3
GA_3 1000	–	94	89	84	3.2	2.6	2.6
	+	83	33	57	4.1	3.0	6.0
Ancymidol 100	–	75	91	88	4.4	3.5	3.6
	+	21	30	41	5.3	5.1	5.6
Ancymidol 250	–	68	94	95	3.3	2.8	2.9
	+	5	62	72	7.7	3.9	4.4
Daminozide 2000	–	70	86	98	3.5	2.8	2.5
	+	10	50	82	7.7	3.8	3.2
Daminozide 5000	–	87	92	93	3.8	3.5	2.7
	+	41	78	64	2.5	6.2	5.2
Chlormequat 2000	–	95	98	77	3.2	3.1	2.9
	+	19	32	62	5.4	6.9	5.0
Chlormequat 5000	–	75	95	95	2.9	2.7	2.8
	+	16	44	44	5.4	4.6	6.2
Phosphon-D 250	–	77	92	84	3.1	2.5	3.2
	+	40	57	41	5.2	4.9	6.0
Phosphon-D	–	64	90	83	3.1	3.0	2.8
	+	52	59	61	3.9	4.1	4.3

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[z] LSD (0.05) for treatment x umbel order x aging = 12%.

[y] LSD (0.05) for treatment x umbel order x aging = 1.0 day.

seed germination was delayed compared to the control by Daminozide at 2000 and Ancymidol at 250 ppm, and hastened by Phosphon-D at 500 and Daminozide at 5000 ppm. Seed aging had no effect on MDG of primary order seeds obtained from plants treated with GA_3, Ancymidol at 100 ppm or Phosphon-D at 500 ppm; but it reduced MDG of seeds from plants treated with Daminozide at 5000 ppm and increased it for seed obtained from plants treated with either Daminozide at 2000 ppm, Ancymidol at 250 ppm, Chlormequat and Phosphon-D at 250 ppm compared with the control (Table 3-9).

Mean days to germination (MDG) of nonaged seed from the primary order of Daminozide (5000 ppm) treated plants, was higher than that of tertiary order seeds. However, there was no significant difference between MDG of primary and secondary order seeds or secondary and tertiary order seeds. On all other treatments, umbel order had no effect on MDG of nonaged seeds (Table 3-9).

Aged seeds of the primary order from GA_3, control and Daminozide (5000 ppm) treated plants had lower MDG compared to tertiary umbel seeds, while those from Daminozide (2000 ppm) and Ancymidol (250 ppm) had higher MDG compared to secondary and tertiary orders seeds. Primary order aged seeds from plants treated with Daminozide at 5000 ppm or Chlormequat at 2000 ppm had faster germination rates (MDG) than seeds produced on the secondary orders, while those from GA_3-treated plants had slower germination rates (MDG) compared to secondary order seeds. Aged seeds from secondary orders of GA_3 and Phosphon-D (500 ppm) treated plants germinated faster than aged tertiary umbel seeds, while those from plants treated with Chlormequat at 2000 ppm germinated slower (Table 3-9).

Experiment II. Seeds harvested from Experiment II were bulked, and the umbel order effect was not examined in this experiment due to the lack of difference between treatment on umbel numbers. Total percentage germination and MDG of the bulk seeds are presented in Appendix Table A-5.

Total percentage germination of nonaged seeds was reduced by Daminozide and Ancymidol at both concentrations, and unaffected by Chlormequat and Phosphon-D. After aging, total percentage germination was reduced by Ancymidol at 250 and Daminozide at 5000 ppm, and increased by Chlormequat and Phosphon-D. Seed aging had no effect on total percentage germination of seed obtained from plants treated with Chlormequat at 5000 ppm and Phosphon-D at 250 ppm. However, seed aging led to reduced total percentage germination of seeds produced on plants treated with any of the remaining treatments (Appendix Table A-6).

Seed aging delayed germination on all treatment (Appendix Table A-6). Seeds from Daminozide, Ancymidol (250 ppm), and Chlormequat (5000 ppm) treated plants had higher MDG compared to control. After aging, MDG was higher from Ancymidol (250 ppm) treated plants, lower from plants treated with Ancymidol at 100 ppm, Chlormequat, or Phosphon-D, and unaffected by Daminozide treatments when compared to the control.

Experiment III. Application of Ancymidol at 100 ppm or Daminozide at 8000 ppm reduced total percentage germination of non aged seeds from the primary order, but had no effect on that from the secondary order when compared to similar seeds from the control (Table

3-10). The remaining treatments had no effect on the germination percentage of nonaged seeds from all umbel orders.

Germination of aged seeds from the secondary orders was improved by Ancymidol at 50 ppm, unaffected by Ancymidol at 25 ppm, Daminozide at 2000 and 4000 ppm, and reduced by Ancymidol at 100 ppm, Daminozide at 100 and 8000 ppm and pruning of the tertiary orders (Table 3-10). Application of Ancymidol at 50 ppm or Daminozide at 2000 ppm to the mother plants, reduced total percentage germination of aged seeds from the tertiary orders compared with a similar treatment from the control. Other treatments had no effect on total percentage germination of aged seeds from tertiary orders. Germination percentage of nonaged seeds from tertiary orders was lower than similar control seeds only from the highest concentration of Daminozide (8000 ppm) (Table 3-10).

Daminozide applied at 8000 ppm was the only treatment that had an adverse effect on MDG of nonaged seeds from the primary order compared to seeds from the primary umbel of the control. Seed aging delayed germination of primary order seeds from all treatments, and the delay was significantly different, compared to the untreated control, with the application of Daminozide at 1000 ppm, 2000 ppm or 8000 ppm, and pruning (Table 3-10).

Application of Ancymidol at 50 ppm or hand pruning of the tertiary umbels significantly increased the germination rate of the nonaged seeds of the secondary orders compared to the control. Germination of aged seeds of secondary orders was delayed by Ancymidol at 25 ppm and Daminozide at 1000 ppm (Table 3-10).

Table 3-10. Effects of mother plant treatments, umbel orders and seed aging on total percentage germination and mean days to germination for Experiment III, fall 1984.

Treatment	Aging	Total percentage germination			Mean days to germination		
		1°	2°	3°	1°	2°	3°
— ppm —		%			days		
Control	-	98[z]	92	100	3.4[y]	4.0	2.6
	+	37	46	43	6.5	6.7	6.1
Ancymidol 25	-	86	92	93	2.7	3.1	3.6
	+	15	41	53	6.5	8.3	6.4
Ancymidol 50	-	95	91	89	2.7	2.9	3.4
	+	28	63	4	6.8	6.0	4.0
Ancymidol 100	-	71	83	92	3.6	3.3	2.8
	+	10	21	35	7.0	6.5	7.5
Daminozide 1000	-	93	95	96	4.1	3.3	3.3
	+	19	29	71	10.3	8.8	6.5
Daminozide 2000	-	87	98	90	3.7	3.1	3.5
	+	14	43	4	7.7	6.7	10.5
Daminozide 4000	-	87	97	96	4.4	4.0	3.5
	+	19	46	44	7.5	6.3	7.5
Daminozide 8000	-	86	87	85	4.8	4.1	4.6
	+	46	30	42	8.7	7.2	8.0
Pruning	-	96	97	-	3.0	2.9	-
	+	23	11	-	8.0	9.5	-

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[z] LSD (0.05) for treatment x umbel order x aging = 11%.

[y] LSD (0.05) for treatment x umbel order x aging = 1.0 day.

The germination rate of non aged tertiary umbel seed was reduced by the application of Daminozide at 8000 ppm, compared to the control. However, the germination rate of the aged seed was reduced by Ancymidol at 100 ppm and Daminozide at 2000, 4000 and 8000 ppm (Table 3-10).

Seedling Growth

Experiment I. Generally, radicle length of the progeny of tertiary umbel seeds was longer than those of primary umbel seeds, regardless of growth regulators or aging treatments (Table 3-11). The only exception was the radicle length of the non aged seed from the control, Daminozide at 5000 ppm and Phosphon-D at both concentrations, where the difference between primary and tertiary umbel was nonsignificant. When compared to secondary umbel, non aged seed of tertiary umbels obtained from those plants treated with GA_3, Daminozide at 2000 ppm, or Chlormequat at 5000 ppm, produced longer radicles than secondary umbel seeds from the same plants. Aged tertiary umbel seeds from the control, or plants treated with GA_3, Ancymidol at 100 ppm, and Phosphon-D had longer radicle lengths compared to aged secondary umbel seeds from the same plants.

Seed aging had no effect on seedling radicle length from primary umbel seeds of the control, GA_3, and Phosphon-D at 250 ppm, secondary umbel seeds of Daminozide at 5000 and Chormequat at 2000 ppm and tertiary umbel seedling of GA_3, Ancymidol at 100 and 250 ppm and Chlormequat at both concentrations.

Table 3-11. The effects of mother plant treatment, umbel order and seed aging on radicle length and hypocotyl length of the progeny seedlings, Experiment I, fall 1983.

Treatment	Aging	Radicle length 1°	Radicle length 2°	Radicle length 3°	Hypocotyl length 1°	Hypocotyl length 2°	Hypocotyl length 3°
— ppm —		cm					
Control	-	1.3[z]	2.1	1.9	3.1[y]	2.4	3.2
	+	0.7	1.0	2.1	2.4	1.9	2.5
GA 1000	-	1.2	3.1	4.5	2.6	3.4	3.9
	+	0.8	1.1	3.2	2.9	2.6	3.9
Ancymidol 100	-	1.8	2.0	2.5	3.1	3.1	3.4
	+	0.5	0.9	1.7	2.6	2.0	2.6
Ancymidol 250	-	1.3	2.5	2.8	3.2	3.0	3.9
	+	0.7	1.3	1.5	2.0	2.4	3.1
Daminozide 2000	-	2.1	2.5	3.4	3.8	2.8	3.6
	+	0.5	1.6	2.4	2.1	2.7	3.6
Daminozide 5000	-	1.8	2.4	2.1	3.1	3.1	3.4
	+	0.6	1.8	2.0	2.4	2.9	3.3
Chlormequat 2000	-	2.5	2.6	3.1	3.0	3.2	3.7
	+	0.5	2.1	1.9	2.4	3.3	3.5
Chlormequat 5000	-	1.6	2.1	3.0	3.3	3.3	3.7
	+	0.6	1.2	1.9	2.5	2.6	3.5
Phosphon-D 250	-	1.8	2.0	2.3	3.4	3.2	3.5
	+	1.2	1.1	2.2	2.6	2.6	3.2
Phosphon-D 500	-	1.7	1.6	2.2	3.0	3.4	3.4
	+	0.8	0.7	2.5	2.5	2.6	2.9

[z] LSD (0.05) for treatment x umbel order x aging = 0.7.

[y] LSD (0.05) for treatment x umbel order x aging = 0.6.

Hypocotyl length of seedling from tertiary umbel seeds was longer than those from primary umbel seeds. This effect of umbel order was more pronounced after seed aging, where most of the treatments had longer hypocotyl lengths from tertiary umbel seeds than primary umbel seeds (Table 3-11). Aging had no effect on hypocotyl length of primary umbel seedling from plants treated with GA_3, Chlormequat at 2000 ppm and Phosphon-D at 500 ppm, but reduced hypocotyl length of primary umbel seedlings from all other treatments. On the secondary umbel, aging reduced hypocotyl length of seedlings produced from plants treated with GA_3, Ancymidol at 100 ppm, Chlormequat at 5000 ppm and Phosphon-D at 500 ppm. Hypocotyl length of tertiary umbel seedlings from the control and those plants treated with Ancymidol at 250 ppm and Phosphon-D at 500 ppm was also reduced by seed aging (Table 3-11).

Seedling fresh weight of non aged primary umbel seeds was reduced by GA_3 and increased by Chlormequat at 2000 ppm, compared to the control. While that of non aged secondary umbel seed was unaffected by Daminozide at 2000 ppm and Phosphon-D at 500 ppm and increased by all other treatments (Table 3-12). Seedling fresh weight of non aged tertiary umbels was increased by GA_3, Ancymidol at 250 ppm, Chlormequat at both concentrations and Phosphon-D at 250 ppm, compared to the control. Unlike radicle length and hypocotyl length, the effect of growth regulator treatments, seed aging and umber order on seedling fresh weight and dry weight, did not follow clear patterns, especially their effect on seedling dry weight.

Table 3-12. The effects of mother plant treatment, umbel order and seed aging on fresh and dry weight of the progeny seedlings, Experiment I, fall 1983.

		Seedling fresh weight			Seedling dry weight		
Treatment	Aging	1°	2°	3°	1°	2°	3°
— ppm —		mg/seedling					
Control	–	12.2[z]	7.7	8.9	0.73[y]	0.26	0.30
	+	5.2	8.0	9.2	0.27	0.33	0.62
GA_3 1000	–	8.9	12.9	22.9	0.62	0.54	0.82
	+	8.2	9.9	14.9	0.47	0.52	0.90
Ancymidol 100	–	13.2	10.4	10.1	0.69	0.65	0.48
	+	6.9	7.9	9.7	0.38	0.39	0.56
Ancymidol 250	–	11.4	11.6	12.6	0.54	0.56	0.47
	+	8.0	9.1	10.7	0.59	0.55	0.53
Daminozide 2000	–	11.5	8.8	10.9	0.50	0.52	0.53
	+	6.1	9.8	11.9	0.37	0.56	0.66
Daminozide 5000	–	10.7	10.9	10.7	0.48	0.52	0.51
	+	6.0	10.7	9.7	0.31	0.50	0.49
Chlormequat 2000	–	16.1	11.7	12.2	0.71	0.60	0.52
	+	7.5	13.1	11.9	0.37	0.56	0.55
Chlormequat 5000	–	11.5	10.3	15.8	0.40	0.50	0.38
	+	6.9	10.6	9.5	0.28	0.47	0.54
Phosphon-D 250	–	11.5	10.1	12.8	0.45	0.45	0.38
	+	7.7	9.5	8.5	0.33	0.42	0.77
Phosphon-D 500	–	10.1	7.5	10.9	0.33	0.23	0.49
	+	7.2	7.5	9.8	0.29	0.19	0.50

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[z] LSD (0.05) for treatment x umbel order x aging = 2.5.

[y] LSD (0.05) for treatment = 0.32, umbel order x aging = 0.25.

Experiment III. The effect of umbel order on seedling radicle and hypocotyl length in experiment 3 folowed the same pattern of experiment 1, with longer radicle and hypocotyl produced by tertiary umbel seeds compared to primary and secondary umbel seeds (Table 3-13). Seed aging had no effect on seedling radicle length from primary umbel seeds obtained from plants treated with Ancymidol at 50 ppm and 100 ppm, Daminozide at 8000 ppm and pruning, while it reduced seedling radicle length from secondary umbel seeds from plants treated with Ancymidol at 100 ppm and increased that of seedlings from the control. The radicle length of tertiary umbel seedlings was reduced by seed aging regardless of the treatment.

Hypocotyl length of seedlings from aged tertiary umbel seeds obtained from plants treated with Ancymidol at 25 ppm and 100 ppm, and Daminozide at 1000, 2000 and 8000 ppm was longer than that from primary umbel seeds from the same plants (Table 3-13). However, there was a significant difference between hypocotyl length from aged primary and tertiary umbel seeds from other treatments.

Seed aging reduced seedling fresh weight from primary umbel seeds produced on plants treated with Ancymidol at 25 ppm, secondary umbel seeds produced on the control or from plants treated with Ancymidol at 50 or 100 ppm, and tertiary umbel seeds from the control and from plants treated with Ancymidol at 25 or 50 ppm and Daminozide at 1000 and 8000 ppm (Table 3-14).

The effect of seed aging on seedling dry weight was more profound on tertiary umbel seedlings (Table 3-14). Aging reduced seedling dry

Table 3-13. The effects of mother plant treatment, umbel order and seed aging on radicle length and hypocotyl length of the progeny seedlings, Experiment III, fall 1984.

Treatment	Aging	Radicle length 1°	Radicle length 2°	Radicle length 3°	Hypocotyl length 1°	Hypocotyl length 2°	Hypocotyl length 3°
— ppm —		cm					
Control	-	5.0[z]	4.0	6.1	3.5[y]	3.8	4.1
	+	4.3	6.7	4.5	4.4	3.0	4.6
Ancymidol 25	-	5.6	4.8	6.9	4.5	3.3	3.6
	+	4.0	5.0	5.2	3.4	3.6	4.2
Ancymidol 50	-	3.7	4.5	5.5	4.0	3.8	3.5
	+	4.2	4.3	3.6	3.7	3.7	3.7
Ancymidol 100	-	4.7	5.4	6.5	4.5	4.1	3.9
	+	4.6	4.5	5.9	3.0	3.4	5.3
Daminozide 1000	-	4.3	3.8	4.2	3.5	3.5	3.6
	+	3.6	3.4	3.4	3.2	3.2	3.8
Daminozide 2000	-	4.4	4.2	6.6	3.5	4.3	4.3
	+	3.3	3.8	5.7	3.6	4.0	5.2
Daminozide 4000	-	4.1	3.7	5.0	4.1	3.7	3.2
	+	3.1	3.2	4.3	3.4	3.3	3.6
Daminozide 8000	-	5.1	4.1	4.6	3.7	3.3	3.7
	+	5.7	3.9	4.2	3.5	3.4	4.1
Pruning	-	4.2	5.1	-	4.3	4.0	-
	+	4.3	5.1	-	4.0	3.5	-

[z] LSD (0.05) for treatment x umbel order = 0.6.
LSD (0.05) for umbel order x aging = 0.3.

[y] LSD (0.05) for treatment x umbel order x aging = 0.5.

Table 3-14. The effects of mother plant treatment, umbel order and seed aging on fresh and dry weight of the progeny seedlings, Experiment III, fall 1984.

Treatment	Aging	Seedling fresh weight			Seedling dry weight		
		1°	2°	3°	1°	2°	3°
— ppm —		mg					
Control	−	12.2[z]	14.7	17.4	0.58[y]	0.61	0.81
	+	14.0	11.3	14.2	0.69	0.60	0.72
Ancymidol 25	−	16.1	11.5	16.7	0.69	0.52	0.84
	+	13.1	15.5	14.1	0.67	0.71	0.71
Ancymidol 50	−	11.3	12.8	15.8	0.45	0.57	0.71
	+	12.2	10.4	12.5	0.59	0.50	0.58
Ancymidol 100	−	16.7	14.5	16.8	0.70	0.73	0.68
	+	17.4	11.1	16.5	0.88	0.52	0.73
Daminozide 1000	−	11.2	13.4	14.0	0.82	0.60	0.62
	+	10.4	12.1	10.7	0.51	0.58	0.53
Daminozide 2000	−	13.3	13.0	17.6	0.61	0.60	0.83
	+	12.0	12.9	16.0	0.56	0.61	0.78
Daminozide 4000	−	11.8	10.9	12.7	0.45	0.52	0.59
	+	9.7	10.0	11.3	0.45	0.46	0.47
Daminozide 8000	−	15.0	11.7	14.1	0.62	0.52	0.69
	+	15.9	10.7	11.8	0.69	0.59	0.57
Pruning	−	13.6	12.9	−	0.51	0.61	−
	+	13.0	12.7	−	0.60	0.57	−

[z] LSD (0.05) for treatment x umbel order x aging = 2.1.

[y] LSD (0.05) for treatment x umbel order x aging = 0.1.

weight of tertiary umbel seedlings from plants treated with Ancymidol at 25 or 50 ppm and Daminozide at 1000, 4000 or 8000 ppm.

Discussion

The objectives of this study were to investigate the possibility of the use of chemical growth regulators as chemical pruning agents to modify seedstalk development in carrot seed plants, and to determine the effect of such modification on seed yield and seed quality.

Gibberellic acid (GA_3), Ancymidol, Daminozide, Chlormequat (CCC), and Phosphon-D were selected for this study based on their reported effects and mode of action. Gibberellic acid causes stem elongation in many rosette and caulescent plants, by increasing cell division in the subapical region of the meristem (Long, 1957; Sachs *et al*., 1959; Bernier *et al*., 1964). Chlormequat, Daminozide, Ancymidol and Phosphon-D are classified as growth retardants, and are believed to be antagonists to gibberellic acid. They inhibit cell division in the subapical zone and thereby inhibit stem elongation (Sachs *et al*., 1960). Gibberellic acid prevents or reverses the inhibition of stem elongation caused by growth retardants (Sachs *et al*., 1960; Sachs and Lang, 1961; Sachs and Kofranck, 1963; Margara, 1961).

The inhibition of stem elongation by growth retardants is achieved through their effects on GA-biosynthesis. Barnier *et al*. (1969), using *Fusarium* reported that CCC inhibited the cyclization of geranylgeranyl pyrophosphate to (-)_Kaurene, an intermediate of gibberellin biosynthesis; but it had no effect on the conversion of (-)-Kaurene to GA. Application of CCC to *Pharbitis nil* plants at anthesis reduced the endogenous GA-like level in the seeds (Zeevaart, 1966b).

Wylie _et al_. (1970) reported an increase in the level of geranylgeranyl pyrophosphate in the root tips of peas by Daminozide (SADH), indicating a disruption of the gibberellin biosynthesis similar to that caused by CCC. On the other hand, Reed _et al_. (1965) suggested that mode of action of Daminozide was in the inhibition of auxin biosynthesis. The inhibition of shoot elongation in dwarf and tall peas by SADH was related to reduced oxidation of tryptamine-2-^{14}C to indoleacetaldehyde-2-^{14}C.

The mode of action of Ancymidol involves the depression of GA-biosynthesis reactions. Using cell-free enzyme system from pea shoot tips and wild cucumber, Coolbaugh and Hamilton (1976) reported that Ancymidol at 10^{-5} m completely blocked the conversion of (-)-Kaurene to Kaurenol. At higher concentration (10^{-3} m) Ancymidol inhibited the incorporation of mevalonic acid-$^{-4}$C into (-)-Kaurene. The effect of Ancymidol on GA-biosynthesis by _Gibberella fujikuro_ showed 97% inhibition of GA production (Shive and Sister, 1976).

Based on their mode of action, and the reported effect of GA on stem elongation in carrots (Hiller and Kelly, 1979), it was hoped that application of chemical growth retardants to carrot seed plants, would result in retardation of seedstalk growth. It is more likely to obtain fewer number of branches on a shorter seedstalk than a longer one. A disruption of the internal hormonal balance of the plant, through the application of growth retardants might result in changes in the branching habit.

Application of GA_3 to carrots following vernalization hastened seed stalk initiation and increased seedstalk height, but had no effect on the number of days to primary umbel anthesis. Induction of stem elongation by GA_3 application is well documented in the literature (Lang, 1956a; Sachs et al., 1960; Sachs and Lang, 1961). If applied after vernalization, giberrellin was reported to increase stem elongation and consequently resulted in flowering in a number of cold-requiring plants including carrots (Lang, 1956c, 1957a). The major problem with GA_3 application to carrots under field conditions is the excessive seedstalk elongation, which might result in lodging and seed yield reduction. Application of GA_3 was also reported to cause an irregular flowering pattern and sterility in some carrot plants (Dickson and Peterson, 1960).

Growth retardants had no effect on number of days to primary umbel anthesis, however, they reduced seedstalk height in all experiments. Reduction of stem elongation is the major response to several growth retardants, including CCC (Margara, 1961; Zeevaart, 1964), SADH (Jaffe and Isenberg, 1966), and Ancymidol (Leopold, 1971; Dick et al., 1974; Sage, 1980). Generally, application of growth retardants after vernalization or complete induction period reduced stem elongation, but had no effect on flowering. Sage and Osada (1966) reported that application of CCC, AMO-1518, Phosphon-D, and SADH after vernalization reduced the final stem height, but did not affect flowering of winter wheat. Similarly, application of CCC or SADH (Zeevaart, 1964, 1966) via the roots of SD Pharbitis after induction period did not inhibit flowering, but stem growth was reduced markedly. A complete inhibition of flower formation was reported only when growth retardants were applied before induction (Suge, 1980).

The total number of umbels per plant was unaffected by GA_3, CCC at 5000 and Phosphon-D at 500 ppm, and reduced by Ancymidol and Daminozide at both concentrations, CCC at 2000 ppm and Phosphon-D at 250 ppm in Experiment I. Branching was unaffected by all chemical regulators in Experiment II. Ancymidol at all three concentrations, Daminozide at the lowest three concentrations and pruning of tertiary umbels reduced the total number of umbels in Experiment III.

Growth retardants were more effective in reducing the number of branches during the fall than the summer. The lack of effectiveness during the summer is attributable to the high greenhouse temperature during the summer (Appendix Table A-2). Extensively high temperature appeared to interfere with the response of carrot plants to growth retardant application. Under growth chamber conditions, seedstalk height and total number of branches of carrot were severely reduced by high temperature (33/28°C). It is possible that high temperature lowers the level of GA. Such original low levels of GA in the control plants would reduce the effectiveness of growth retardants due to the lack of substrate for their action. This explanation is supported by the results of Hiller _et al_. (1979) who reported a decrease in the effects of CCC and SADH on carrot seedstalk height as the temperature increased from 21/15°C to 32/27°C.

Initiation of lateral branches is determined by many factors and the interrelationship between these factors. Distribution of growth substances and competition for nutrients are two of the most important factors in the formation of lateral branches in many herbaceous plants. The apical meristem of lateral buds is apparently influenced by these factors in the same way the apical meristem of the terminal bud is influenced by them (Esau, 1982).

Tucker and Mansfield (1973) reported a strong influence of auxin, abscisic acid and cytokinin on lateral branch formation in Xanthium. Gibberellin did not appear to play a major role in lateral bud formation and apical dominance, according to their data; but it might be important for bud extension following its release.

The nature of the mechanism that controls branch formation in rosette plants, especially umbelliferous plants, has not received much attention and still remains unclear. The apical bud does not appear to have any inhibitory role on the development of secondary umbels. Umbel primordia differentiation in carrots was reported to begin by the time macroscopic seedstalk elongation was evident (Tsukamoto et al., 1957; Borthwick et al., 1931a).

The present data suggest a possible role for growth regulator in the initiation and development of lateral branches in carrots. Since the number of umbels is determined early in the development of seedstalks it could be speculated that these chemicals act by modifying the internal hormonal levels in the plant; possibly through their effects on GA biosynthesis or by inhibiting the early differentiation of branches, through reducing cell elongation and division.

There are two major differences between the four retardants used in the present study, i.e., Ancymidol, CCC, Daminozide and Phosphon-D. First among the four, Ancymidol inhibits stem elongation of a wide spectrum of plants and completely blocks GA synthesis (Cathy, 1975). Daminozide was reported to be more active in inhibiting stem elongation in many plants, compared to CCC, while Phosphon-D was the least effective in inhibiting stem elongation. Second, CCC and Phosphon-D were reported to have inhibitory effects on auxin level in plant tissues (Kraishi and Muir, 1963; Leopold, 1971). Ancymidol had no effect on auxin induced growth, but uniquely inhibits gibberellin-induced growth of lettuce hypocotyl (Leopold, 1971). Daminozide was reported to inhibit GA biosynthesis and also reduced the level of indoleacetaldehyde, a precursor of auxin (Reed et al., 1965; Wylie et al., 1970).

The increase in the concentration of Ancymidol from 25 ppm to 100 ppm had no effect on branching and seedstalk height, indicating that the maximum inhibition was obtained by the lowest concentration. Unlike Ancymidol, Daminozide showed no definite pattern with increased concentration from 1000 to 8000 ppm, however, there was a clear reversal effect at the very high concentration. The lack of consistency of Daminozide effects with increased concentration is one of the major problems of this chemical (Cathy, 1975). The increase in Daminozide concentrations was not followed by a subsequent increase in its effectiveness on many plants, and in most plants, such increase or decrease in its concentration resulted in erratic effects. This makes the prediction of response to Daminozide a rather difficult and in many cases, unattainable goal.

Seed yield was reduced by Ancymidol in Experiments I and III, Daminozide at 2000 ppm and Phosphon-D at 500 ppm in Experiment II, and Daminozide at 1000, 4000 and 8000 ppm in Experiment III. The reduction in seed yield by Ancymidol and Daminozide is mainly due to the decrease in the number of umbels. Primary umbel size was also reduced by Ancymidol. This reduction in seed yield could be compensated, in practical field situations, by increasing plant population per unit area. However, both chemicals showed no difference in seed yield when compared to pruning of the tertiary umbels.

Although chemical growth regulators were effective in reducing the total number of umbels per plant, they did not improve seed germination. The most effective chemicals in reducing the number of umbels in experiment 1, i.e., Ancymidol and Daminozide, did not improve seed germination, and neither chemical pruning nor hand pruning did improve seed germination and seedling growth in experiment III.

Hand pruning was reported to improve seed germination in carrot, by eliminating tertiary umbel seeds, which were believed to be of low quality (Hagije, 1954, Krarup _et_ _al_., 1976; Mijagi, 1956). Daminozide was expected to improve seed germination, since it reduced the amount of seeds from the tertiary umbels.

The lack of improvemeent in seed germination by chemical or hand pruning was attributed to the fact that seeds on all umbel orders were harvested after they reached maturity; which eliminated seed maturity effects on seed germination. Seeds were produced under ideal environmental conditions, with less chance of shattering under greenhouse conditions. Seeds which developed on the tertiary umbels were larger, had higher germination and produced seedlings with longer radicles, in both experiments 1 and 3; compared to seeds from primary and secondary umbels. Since both chemical and hand pruning reduced the amount of the superior seed from tertiary umbels and increased the amount of poor seed from primary and secondary umbels, the ineffectiveness of such treatments in improving seed germination is justifiable. On the other hand, the untreated control had higher amounts of seed from tertiary umbels compared to pruned plants.

The results of this study are in contrast to most of the published work on carrot seed production. Seeds from the primary umbels were reported to be larger and had higher germination compared to secondary and tertiary umbel seeds (Borthwick, 1931a; Jacobsohn and Globerson, 1980; Krarup and Villanuevaa, 1977a). However, the effect of umbel order in all these studies was confounded with the effect of seed maturity. None of the above studies allowed tertiary umbel seeds to reach full maturity.

Mature seeds from secondary umbels gave larger plants than seeds of the same size from primary umbels (Gray and Steckel, 1980). Similarly, mature seed from secondary umbels had similar germination to mature seed from primary umbels (Gray, 1979). Thus, harvesting seed at full maturity appeared to eliminate the effect of seed position on seed quality in carrot.

Perhaps the most accurate and detailed studies on carrot seed quality were the ones reported by Hawthorn _et al_. (1962). They reported that the germination capacity of seeds harvested 35 or more days after anthesis on each umbel did not differ significantly between umbel orders. Thus, harvesting seed at its full maturity appeared to eliminate the effects of umbel orders on seed quality in carrots.

Based on the results of the present study, it could be concluded that delaying the harvest date in carrot would ensure the production of high quality seeds from tertiary umbels. Franklin (1953) and Hawthorn _et al_. (1962) recommended delaying carrot seed harvesting until tertiary umbel seeds reached maturity. Under field production, a delay in carrot seed harvest might result in some seed loss due to shattering from primary umbels. However, such seed loss is unlikely to reduce seed yield, due to the compensation by the tertiary umbel seeds. The primary umbel contribution ranged between 5 to 15% of seed yield, while the tertiaries contributed about 36 to 50% (Borthwick, 1931a; Hawthorn _et al_., 1962; Krarup and Villanueva, 1977a). An increase in carrot seed yield as a result of delaying harvest until tertiary umbel seed reached maturity was reported by Castra and Andrews (1970).

Carrot seed fields are usually harvested during August and early September, when secondary umbel seeds reach maturity. Delaying the harvest for 30 days would ensure the maturation of all tertiary umbel seeds. However, the chances of an early frost increases with delaying seed harvest until October. A delay in harvest date, accompanied by mechanical or chemical destruction of primary umbel would result in the production of uniform crop maturity, high seed quality and eliminate seed shattering in the field.

Summary

The objectives of this study were to investigate the possibility of the use of chemical growth regulators as chemical pruning agents to modify seedstalk development in carrot seed plants, and to determine the effects of such modification on seed yield and seed quality.

Ancymidol at 100 or 250 ppm, and Chlormequat (CCC) at 2000 or 5000 ppm, were applied as soil drench during fall 1983 (experiment 1) and summer 1984 (experiment 2), at 20 ml/pot for Ancymidol and 200 ml/pot for CCC. Daminozide at 2000 or 5000 ppm and Phosphon-D at 250 or 500 ppm were applied to the growing points at 1 ml/plant in both experiments. Gibberellic acid at 1000 ppm was applied to the growing points at 1 ml/plant in experiment 1.

In experiment III (fall 1984), Ancymidol at 25, 50 or 100 ppm and Daminozide at 1000, 2000, 4000 or 8000 ppm was applied to the growing points at 1 ml/plant. Pruning of tertiary umbels was introduced as another treatment in this experiment. Ancymidol and CCC were applied twice weekly for 2 weeks in all three experiments, while the other chemicals were applied twice weekly for 4 weeks.

The number of days to primary umbel anthesis was unaffected by all treatments in all experiments. Seedstalk height was significantly increased by GA_3 and reduced by all growth retardants. Ancymidol, Daminozide, CCC at 2000 ppm and Phosphon-D at 250 reduced the total number of umbels per plant in Experiment I, while Ancymidol at all

concentrations and Daminozide at the three lowest concentrations along with pruning reduced umbel numbers in Experiment III. The number of umbels was unaffected in Experiment II.

Total seed yield was reduced by Ancymidol in Experiment I, Daminozide at 2000 ppm and Phosphon-D at 500 ppm in Experiment II, and by Ancymidol at all concentrations and Daminozide at 2000 and 8000 ppm in Experiment III. When compared to hand pruning, however, Ancymidol and Daminozide had no effect on seed yield in Experiment III.

The distribution of seed yield between different umbel orders was not affected by any of the treatments. Daminozide, however, had a tendency towards increasing the amount of seed contributed by the primary and secondary umbels to the final seed yield and reducing that contributed by tertiary and quaternary umbels.

Despite the reduction in total number of umbels by chemical and hand pruning, seed germination was not improved by either method. That seed quality was not improved was attributed to the reduction by both methods of the high quality seed produced on the tertiary umbels, and the increase of poor quality seed produced on the primary and secondary umbels by both treatments. Tertiary umbel seeds were the largest seeds, had the highest germination and produced the longest seedlings, compared to primary and secondary umbel seeds.

Delaying carrot seed harvest until tertiary umbel seeds reach maturity is highly recommended to increase seed yield and improve seed quality. Such practice would cause shattering of primary umbel seeds. However, this loss could be compensated for by the increase in the yield of tertiary umbels, which contribute higher amounts of seed than primary umbels.

CHAPTER IV
CONTROL OF SEEDSTALK DEVELOPMENT, SEED YIELD AND SEED QUALITY IN CARROTS BY TEMPERATURE DURING SEED CROP GROWTH

Introduction

The effect of temperature on flower initiation, flowering and seed production of many agronomic and horticultural crops has long been recognized (Thompson, 1939; Went, 1953). Seed yield, seed quality and seedling vigor are closely correlated with the growing environment of the mother plant (Austin, 1972). Among the several environmental factors, temperature appears to be the primary factor influencing the seed crop from the vegetative phase to all stages of seed development and maturation.

It has been reported that warm to high seed maturation temperatures increased the germination capacity of freshly harvested seeds of sugarbeet (Wood et al., 1980), lettuce (Harrington and Thompson, 1952; Koller, 1962), barley (Khan and Laude, 1969), bean (Gloyer, 1932), forage grasses (Akpan and Bean, 1977), hybrid rose (von Abrams and Hand, 1956) and alfalfa (Walter and Jensen, 1970), compared to seed which matured under cool temperatures.

In carrot seed production, the reported work on temperature effects has dealt mainly with the early stages of the seed crop development such as flower initiation, seedstalk development and sex expression.

Sakr and Thompson (1942) reported that a greenhouse growing temperature of 10 to 15°C following vernalization resulted in 60 to 100% flowering and was more favorable to reproductive growth in the cultivar 'French Forcing' than 15 to 21°C or 21 to 27°C. Dickson and Peterson (1958) found that plants grown at 13°C bolted earlier and in higher percentages than those grown at 18°C, following cold storage of the roots.

Quagliotti (1967) studied the temperature modifying influence on seedstalk development and sex expression in the cultivar 'Amsterdam Forcing.' The results of her study showed that at high temperature (26°C), plants flowered earlier, but the quality of the seedstalk developed was very poor. At the low growing temperature (14°C) both the total number of flowers and the number of fertile hermaphroditic (bisexual) flowers were more than twice the number obtained at 26°C. The proportion of male flowers increased with temperature and was significantly higher at 26°C. Eisa and Wallace (1969) reported that high temperature increased petaloidy in carrots and decreased seedstalk height.

The purpose of this study was to investigate the effect of different growing temperatures on seedstalk development, seed yield and seed quality in carrots.

Materials and Methods

Stecklings of carrot cv. 'Hicolor-9' were raised, treated and vernalized as described in Chapter III. The following experiments were conducted between 1983 and 1985.

Experiment I: The Influence of Different Growing Temperatures on Seedstalk Development, Seed Yield and Seed Quality

The objective of this experiment was to study the effect of temperature during seed crop growth on seedstalk development, seed yield and seed development in carrots.

Carrot stecklings were potted in 8 liter pots filled with 3:1 peat:perlite mixture in the greenhouse. After the beginning of seedstalk initiation, uniform plants were transferred to growth chambers (Conviron E-15), in which the day/night temperatures were set at 33/28°C, 28/23°C, 25/20°C, 23/18°C, 20/15°C, and 17/12°C. Light intensity of 775 and 600 $uE/m^2/s$ at primary umbel level and pot level, respectively, and photoperiod, 14 hours day and 10 hours night, were the same in all chambers. Plants were fertilized with 20:9:17 (N:P:K) every week, and irrigated when required. Relative humidity was maintained at 90% during vegetative and early reproductive stages, then adjusted to 40% when seeds on the primary umbel started to mature. The experiment was a completely randomized design, with 10 replications (plants) in each chamber.

Plants were tagged at the date of anthesis of the first flower on the primary umbel. Pollination was by hand, in the morning and late afternoon. Seeds were harvested when seeds on the tertiary umbels reached maturity (i.e., after 55, 70 and 90 days from primary umbel anthesis for 33/28°C, 28/33°C and all remaining treatments, respectively), threshed, cleaned by hand and stored at 10°C and 20% R.H. Germination and vigor evaluations were made as described in Chapter III.

Embryo extraction was done by placing the sample of seed in distilled water for four hours, to soften the outer tissues. The caruncle was cut off each seed and the embryos were carefully squeezed out by applying gentle pressure to the seed with the back of a scalpel blade. Four replications of each treatment with 25 seeds per replication were used. The embryos were measured at 40x magnification under a binocular.

Experiment II: The Influence of Temperature Stress During Various Growth Stages on Seed Yield and Seed Quality

The objective of experiment 2 was to investigate the influence of a brief exposure to high temperature at different stages of seed development on seed yield and seed quality in carrots.

Carrot stecklings were potted in 8 liter pots in 3:1 peat:perlite mixture; in growth chambers set at 20/15°C day/night. Light intensity and photoperiod were similar to those of experiment I. After seedstalk initiation, uniform groups of plants were selected for the treatments. Growth chambers were reset either at 33/28°C or 20/15°C (day/night). Plants were exposed to one of the following treatments

1. Continuous high temperature (33/28°C),
2. Continuous low temperature (20/15°C),
3. Transfer to high temperature at flower anthesis,
4. Transfer to high temperature at early seed development (10 days after flower anthesis begins), or
5. Transfer to high temperature at late seed development (30 days after flower anthesis begins).

After exposure to high temperature (33/28°C) for 10 days, plants in treatments 3, 4, and 5 were returned to low temperatures (20/15°C) until harvest. Each treatment consisted of six replications.

Because of the complexity of flowering, each individual umbel was tagged, and any umbels undergoing the high temperature treatment were harvested and used for subsequent seed quality testing. Seed yield and number of seeds per single umbel on each order were counted. Seed germination and vigor were evaluated as previously described.

Results and Discussion

Experiment I: The Influence of Different Growing Temperatures on Seedstalk Development, Seed Yield and Seed Quality

Flowering and seedstalk development. The number of days to primary umbel anthesis decreased linearly as developmental temperature increased from 17/12°C to 33/28°C (Table 4-1). Flowers on the primary umbel reached anthesis after an average of 48 days from planting at 33/28°C compared to an average of 77 days at 17/12°C. Quagliotti (1967) reported that plants grown at 26°C flowered earlier than those which were grown at 14°C. Similarly, Hiller and Kelly (1979) found that bolting was quicker and umbel formation was completed earlier in plants kept at 27/21°C or 32/27°C than at 21/15°C.

Growing temperature had a significant effect on seedstalk height. High temperature (33/28°C) drastically reduced the final seedstalk height compared to low temperatures. However, the relationship between growing temperature and seedstalk height was non-linear (Table 4-1). Similar effects of post-vernalization temperature and after-flowering temperature stress was reported by Hiller and Kelly (1979)

Table 4-1. Effect of different temperatures during seed crop growth on number of days to primary umbel anthesis, seedstalk height, number of umbels per each order and total number of umbels per plant.

Day/night temperature	No. days to primary anthesis	Seedstalk height	Number of umbels/order 2°	3°	4°	Total number per plant
°C		cm				
17/12	77	72	8	19	22	50
20/15	71	68	7	19	18	46
23/18	62	79	7	16	14	38
25/20	64	63	6	17	16	40
28/23	53	66	6	13	14	34
33/28	48	55	5	10	11	28
Signif.[z]	L**	NS	L**	L**	L**	L**

[z] Significant effects were linear (L) or quadratic (Q) at the 5% (*) or 1% (**) level.

and Quagliotti (1967), respectively. Dickson and Peterson (1958) reported that reproductive development in carrots was hastened by higher temperature (27/21°C). The effects of high temperature on seedstalk height could be attributable in part to the decrease in gibberellin-like activity in the shoot apex at excessively high temperature. The results obtained by Hiller et al. (1979) showed a reduction in gibberellin-like activity determined by the lettuce hypocotyl bioassay, with the increase in post-vernalization temperature from 21/15°C to 32/27°C.

Total number of umbels per plant and the number of umbels on the secondary, tertiary and quaternary umbels decreased linearly with the increase in the growing temperature from 17/12°C to 33/28°C (Table 4-1). The number of umbels on the secondary, tertiary and quaternary orders was reduced by about 38, 47 and 50%, respectively, while the total number of umbels per plant was reduced by about 44% at 33/28°C compared to 17/12°C. The increase in growing temperature from 17/12°C to 25/20°C had no effect on the number of umbels on the secondary and tertiary orders and total number of umbels per plant, however, an increase in temperature from 17/12°C to 23/18°C significantly reduced the number of umbels on quaternary orders. This progressive decrease in umbel number at the higher orders indicates an increase in the effect of high temperature on branching with the increase in the time of exposure to high temperature.

The results of the present study agree with the results of Hiller and Kelly (1979) who reported that development of lateral branches was greatly reduced on plants grown at high greenhouse temperatures, which decreased the total number of umbels. However, both studies contradict the findings of Quagliotti (1967) who reported a greater number of umbels at the higher temperature. The variation between the results could be explained by the rather low temperatures (14-26°C) and the use of constant instead of diurnal temperature in Quagliotti's study, beside the early termination (before the completion of tertiary umbels initiation) of her experiment.

Effects of growing temperature on seed yield. Seed yield expressed as seed weight per plant, seed weight per umbel order, total seed number per plant and seed number per umbel order decreased drastically as the temperature during seed development increased from 20/15°C to 33/28°C (Table 4-2). The reduction in seed weight per plant, seed weight per umbel order, was linear with the increase in temperature. The only exception was for quaternary umbel seed weight which decreased with the increase in temperature from 17/12°C to 33/28°C in a nonlinear fashion because such small amounts of seed were produced. Total seed number per plant and seed number on each umbel order was affected by growing temperatures in a similar pattern to seed weight. The highest seed yield was obtained at 20/15°C and the lowest yield was obtained at 33/28°C. Plants which were kept at 33/28°C were almost barren, with very few seeds on them. An increase in the growing temperature above 20/15°C resulted in a reduction in both seed weight and seed number per plant, while a decrease in temperature below 20/15°C resulted in a reduction in total seed weight per plant, without an effect on seed weight or seed number on each umbel order.

Table 4-2. Effect of different temperatures during seed crop growth on seed yield (weight and number) per each umbel order and total yield per plant.

Day/night temperature	Umbel order				Total per plant
	1°	2°	3°	4°	
— °C —					
	seed weight (gm)				
17/12	3.3	4.8	2.3	0.22	10.7
20/15	4.8	6.6	3.4	0.47	15.4
23/18	1.4	4.9	1.2	0.01	7.5
25/20	1.3	3.1	1.0	0.42	5.8
28/23	0.7	1.8	0.5	0.17	3.1
33/28	0.1	0.2	0.1	0.00	0.3
Signif.[z]	L*	L**	L*	NS	L*
	seed number				
17/12	999	1778	946	84	3806
20/15	1843	2954	1202	214	6201
23/18	686	2780	559	5	4029
25/20	517	1386	391	110	2495
28/23	389	1087	221	77	1774
33/28	69	174	25	0	268
Signif.[z]	NS	NS	NS	NS	NS

[z] Significant effects were linear (L) or quadratic (Q) at the 5% (*) or 1% (**) level.

Part of the reduction in seed yield caused by high growing temperature could be due to poor pollen viability and/or increased male sterility in plants grown at high temperatures. The viability of pollen was reported to be higher when carrot plants were grown under low temperature (Quagliotti, 1967). High occurrence of petaloidy and a decrease in the ratio of hermaphroditic to male flowers may occur at high temperatures as reported by Eisa and Wallace (1960) and Quagliotti (1967).

Yield of onion seed from crops grown at higher temperatures (20–30°C) was less than that from crops grown at lower temperatures (Gray and Steckel, 1984). Poor seed set at high temperatures in onions was associated with pollen sterility and/or abnormal embryo and endosperm development caused by excessively high temperatures (Chang and Struckmeyer, 1975, 1976a, 1976b).

Seed which developed at the highest temperature (33/28°C) had the lowest 1000-seed weight, while those which developed at intermediate temperatures (23/18°C or 25/20°C) had the highest 1000-seed weight (Table 4-3). Averaged over all temperature treatments, tertiary umbel seeds had the highest 1000-seed weight, while there was no difference between seeds which developed on the primary and secondary umbels nor between those on the secondary and tertiary umbels. Reduction in seed weight and size with increasing growing temperatures has been reported in many seed and grain crops (Akpan and Bean, 1977; Gray and Steckel, 1984; Wood et al., 1980).

Table 4-3. Effect of different temperatures during seed crop growth on 1000-seed weight (gm) at each umbel order.

Day/night temperature	Primary umbel	Secondary umbel	Tertiary umbel
°C		gm	
17/12	2.46	2.59	2.44
20/15	2.48	2.46	2.52
23/18	2.91	2.41	1.61
25/20	2.67	3.28	3.53
28/23	2.74	2.42	2.26
33/28	2.14	2.37	2.37
Signif.[z]	L**Q**	Q**	Q**

[z] Significant effects were linear (L) or quadratic (Q) at the 5% (*) or 1% (**) level.

The effects of growing temperature on seed weight (Table 4-3) are less marked than its effects on seed number (Table 4-2), which suggests that seed yield reduction in carrots, due to high temperature stress, is largely a result of decrease in seed number rather than individual seed weight.

Seed germination and seedling growth. Total percentage germination with the standard germination test, of primary umbel seed, was reduced at growing temperatures of 33/28°C and 17/12°C compared to 20/15°C, 23/18°C, 25/20°C and 28/23°C (Table 4-4). Germination of secondary and tertiary umbel seeds was only reduced at developmental temperature of 33/28°C.

After accelerated aging, germination of primary umbel seeds was reduced at all developmental temperatures. The reduction in germination was more severe at developmental temperatures of 17/12°C, 25/20°C, and 33/28°C, compared to 20/15°C, 23/18°C, and 28/23°C. Germination of the secondary umbel seeds was also reduced at all developmental temperatures after accelerated aging. However, the effects of aging were less severe when compared to those of the primary umbel seeds. Secondary and tertiary umbels seeds which developed at 33/28°C had the lowest germination after aging.

Tertiary umbel seeds which developed at 20/15°C were unaffected by accelerated aging, while germination of seeds developed under other developmental temperatures was significantly reduced by accelerated aging. Averaged over umbel orders and aging seeds which developed at growing temperatures of 20/15°C and 23/18°C had the highest germination, while those which developed at 33/28°C and 17/12°C had

Table 4-4. Effect of different temperatures during seed crop growth, umbel order and seed aging on total percentage germination and mean days to germination (MDG) at 25°C.

Day/night temperature	Primary umbel		Secondary umbel		Tertiary umbel	
	Non-aged	Aged	Non-aged	Aged	Non-aged	Aged
°C	Total percentage germination^z					
17/12	84	05	98	48	96	45
20/15	100	41	98	62	94	86
23/18	97	63	95	60	99	56
25/20	94	07	99	64	91	20
28/23	94	33	99	62	94	61
33/28	53	17	71	05	79	10
Signif.^{y}	L** Q*	Q*	L* Q*	L** Q**	L** Q**	L**
	Mean days to germination^x					
17/12	4.3	7.8	4.1	8.1	3.5	7.7
20/15	2.7	7.5	2.7	5.7	4.2	7.9
23/18	2.3	5.9	3.5	6.8	2.9	5.9
25/20	3.1	8.0	2.6	6.8	3.3	7.3
28/23	3.6	8.0	3.6	8.1	3.9	7.0
33/28	4.2	7.8	4.5	8.1	3.4	9.8
Signif.^{y}	Q**		L** Q**	Q*		L** Q**

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[z] LSD (0.05) for temperature x umbel order x aging = 10%.

[y] Significant effects were linear (L) or quadratic (Q) at the 5% (*) or 1% (**) level.

[x] LSD (0.05) for temperature x umbel order x aging = 1.1 days.

the lowest germination. Seed germination on all umbel orders with the standard germination test or accelerated aging increased quadratically with increasing growing temperatures (Table 4-4). Thomas and Raper (1975a, b) reported that tobacco seeds produced from mother plants which were grown under high temperatures (30/26°C) had a lower germination percentage that those from plants given low temperatures (22/18°C). The germination of freshly harvested barley seeds was depressed following heat stress due to severe thermal injury to the seed (Khan and Maude, 1968). On the other hand, moderately warm temperatures have been reported to increase seed germinability by many workers (Evenari, 1965; Koller, 1962; Stearns, 1960). The speed of germination, with standard germination test, of the primary and secondary umbel seeds was delayed at developmental temperatures of 33/28°C and 17/12°C compared to other treatments (Table 4-4). Germination of tertiary umbel seeds was most rapid in seed produced at 23/18°C. There was no difference among the other developmental temperatures.

After accelerated aging, germination of seed produced on all three umbel orders was delayed. The delay in germination was usually least on seeds which developed at 23/18°C (Table 4-4). Tobacco seeds produced at higher temperatures (30/26°C) were slower to germinate than those produced under low temperatures (22/18°C) (Thomas and Raper, 1975a, b). Similarly, low temperatures during seed development (15/10°C) resulted in a low rate of germination of many forage grasses (Akpan and Bean, 1977).

The progeny of seeds which developed at high temperatures (33/28°C) had the shortest radicles and hypocotyls and the lowest seedling fresh and dry weights on all umbel orders (Table 4-5). Seeds which developed at 25/20°C produced seedlings with the highest vigor. These findings agree with the results reported by Akpan and Bean (1977) and Thomas and Raper (1975a, b), in that the largest seedlings of forage grasses and tobacco were always produced by seed which developed at low temperatures compared to those developed at high temperature.

Embryo length increased linearly with the increase in developmental temperature from 17/21°C to 25/20°C, then decreased with the increase in temperature from 25/20°C to 33/28°C. This quadratic relationship between embryo length and developmental temperature was similar on all umbel orders (Table 4-5). The longest embryos were produced at 25/20°C while the shortest embryos were produced at 17/12°C or 33/28°C depending on umbel orders. Akpan and Bean (1977) reported that ovary width and length in grasses were reduced as the temperature increased from 15/10°C to 25/20°C.

The decrease in embryo size at low temperatures could be due to the low growth rate at very low temperatures, while that at high temperatures could be attributed to a rapid growth rate leading to a shorter developmental period. High temperatures accelerated initial grain growth rate in cereals but shorten the grain growth period (Sofield et al., 1977). This shorter grain-filling duration was compensated by faster filling rate under mild stress but not under severe temperature stress.

Table 4-5. Effect of different temperatures during seed crop growth and umbel order on seedling length and weight of the progenies.

Day/night temperature	Primary umbel	Secondary umbel	Tertiary umbel
°C		Radicle length (cm)	
17/12	5.8	6.1	7.2
20/15	6.7	6.3	6.4
23/18	6.3	6.4	7.1
25/20	5.9	7.0	7.7
28.23	7.0	6.4	5.7
33.28	1.9	3.3	5.1
Signif.[z]	L** Q**	L** Q**	L** Q**
		Hypocotyl length (cm)	
17/12	5.5	6.2	6.5
20/15	6.4	6.8	6.4
23/18	6.4	6.7	6.6
25/20	7.0	7.1	7.6
28/23	7.0	6.8	7.0
33/28	4.3	5.5	5.8
Signif.[z]	L** Q**	L** Q**	Q**
		Seedling fresh weight (mg)	
17/12	22.5	25.2	28.2
20/15	22.5	255	24
23/18	24.5	23.9	24.9
25/20	29.1	28.3	32.6
28/23	24.4	24.5	22.6
33/28	10.7	14.6	21.4
Signif.[z]	L** Q**	L** Q**	L** Q**
		Seedling dry weight (mg)	
17/12	1.06	1.21	1.22
20/15	0.99	1.09	1.18
23/18	1.03	1.07	1.11
25/20	1.22	1.09	1.29
28/23	1.03	1.05	0.96
33/28	0.44	0.61	0.84
Signif.[z]	L** Q**	L** Q**	L** Q**

[z] Significant effects were linear (L) or quadratic (Q) at the 5% (*) or 1% (**) level.

Table 4-6. Effect of different temperatures during seed crop growth and umbel order on embryo length.

Day/night temperature	Primary umbel	Secondary umbel	Tertiary umbel
—— °C ——		—— Embryo length (mm) ——	
17/12	1.06	1.51	1.51
20/15	1.73	1.74	1.34
23/18	1.83	1.72	1.72
25/20	2.28	2.35	1.79
28/23	1.69	1.59	1.51
33/28	1.61	1.60	1.10
Signif.[z]	L** Q**	L** Q**	L** Q**

[z] Significant effects were linear (L) or quadratic (Q) at the 5% (*) or 1% (**) level.

Experiment II: The Influence of Temperature Stress During Various Growth Stages on Seed Yield and Seed Quality

Seed yield. Seed weight and seed number of primary and secondary umbels were reduced by short exposure to high temperature at anthesis, early in seed development or continuous high temperature compared to continuous low temperature (Table 4-7). While seed weight of tertiary umbels was not affected by high temperatures at anthesis, seed number was reduced by exposure to high temperature at anthesis, early in seed development or continuous high temperatures. However, the difference in tertiary umbel seed number between the previously mentioned three treatments and exposure to high temperature late in seed development was not significant.

The above results suggest that high temperature affects seed yield in carrots primarily through its effects on microsporogenesis and megasporogenesis. The start of anthesis coincides with pollen grain development and germination, while early stages of seed development coincides with ovule development and endosperm division (Borthwick, 1931; Gray et al., 1984). The effect of high temperature on pollen grain development and germination and pollen tube growth has been demonstrated for bean (Halterlein et al., 1980), onion (Chang and Struckmeyer, 1976a), rice (Stakae and Yoshida, 1978), maize (Herrerd and Johnson, 1980) and tomato (Smith, 1932).

The possibility that high temperatures have some effect on megasporogenesis cannot be ruled out. A detrimental effect of high temperature stress on zygote formation and ovule development have been

Table 4-7. Effect of stage of exposure to high temperature (33/28°C) on average seed weight and seed number per single umbel on primary, secondary and tertiary orders.

Stage of exposure	Primary order	Secondary order	Tertiary order
	Seed weight (gm)		
Continuous low (20/15°C)	4.2	0.8	0.18
Continuous high (33/28°C)	0.4	0.3	0.03
Anthesis	0.2	0.1	0.12
Early seed development	0.1	0.4	0.09
Late seed development	2.6	1.3	0.14
LSD (0.05)	1.3	0.4	0.07
	Seed number		
Continuous low (20/15°C)	2156	400	136
Continuous high (33/28°C)	223	132	12
Anthesis	142	50	50
Early seed development	84	197	36
Late seed development	1182	524	69
LSD (0.05)	585	177	75

reported for sorghum (Dhpote, 1984), citrus (Takagi et al., 1982), bean (Ormrod et al., 1967) and onion (Chang and Struckmeyer (1977).

High temperature stress reduced 1000-seed weight, when the time of brief exposure was at anthesis early or late in seed development, or under continuous exposure to high temperature (Table 4-8). This effect was more profound on the primary umbels, since they were the ones which were exposed to temperature stress for the longest duration. Exposure of secondary and tertiary umbels was not as drastic due to the complexity of branching in carrots and the greater numbers of florets produced as mentioned previously (Chapter 3).

The reduction in seed weight at maturity due to high temperature stress early in seed development might be due to a reduction in cell size caused by the early cessation of growth at high temperatures. Small grain size in wheat ripened under high temperatures was associated with a reduction in cell size (Hoshikawa, 1962); a similar effect of high temperatures on leaf cells of *Vicia faba* was reported by Auld et al. (1978).

Seed germination and seedling growth. Germination of non-aged seeds produced on primary and secondary umbels was severely reduced when parent plants were continuously exposed to high temperature (Table 4-9). High temperature at anthesis, early or late seed development had no effect on the germination of primary or secondary umbel seeds. Germination of tertiary umbel seeds was similar in seeds produced under continuous high or low temperature and greater in seeds that were exposured to high temperature at anthesis, early or late in seed development compared to that produced under continuous temperature.

Table 4-8. Effect of stage of exposure to high temperature (33/28°C) for 10 days on 1000-seed weight (gm).

Stage of exposure	Primary order	Secondary order	Tertiary order
	gm	gm	gm
Continuous low (20/15°C)	4.20	2.97	2.96
Continuous high (33/28°C)	2.91	2.76	2.74
Anthesis	3.29	3.25	3.08
Early seed development	2.84	2.89	2.58
Late seed development	2.49	2.71	2.44
LSD (0.05)	0.34	0.27	0.15

Table 4-9. Effect of stage of exposure to high temperature (33/28°C), umbel order and seed aging on total percentage germination and mean days to germination.

Stage of exposure	Primary umbel		Secondary umbel		Tertiary umbel	
	Non-aged	Aged	Non-aged	Aged	Non-aged	Aged
— °C —	Total percentage germination^z					
Continuous low (20/15°C)	98	21	92	48	80	35
Continuous high (33/28°C)	54	08	69	05	78	10
Anthesis	90	03	94	27	95	34
Early seed development	96	10	96	12	93	20
Late seed development	92	75	89	66	95	21
	Mean days to germination^y					
Continuous low (20/15°C)	3.3	11.1	3.7	7.7	3.9	9.2
Continuous high (33/28°C)	3.4	8.0	2.8	9.4	3.4	8.7
Anthesis	3.3	9.7	2.7	9.2	3.0	8.4
Early seed development	2.8	9.4	3.0	8.7	4.4	7.2
Late seed development	3.8	6.4	3.4	6.2	4.0	9.2

^{z}LSD (0.05) for stage x umbel order x seed aging = 10%.

^{y}LSD (0.05) for stage x umbel order x seed aging = 1.1 days.

After accelerated aging, primary and secondary umbels seeds exposed to high temperature late in their development had the highest germination, while those produced under continuous high temperature or exposed to high temperature at anthesis or early in their development had the lowest germination compared to those developed under continuous low temperatures (Table 4-9). After aging, seed on the tertiary umbel germinated poorly regardless of the temperature treatment.

High temperature stress had no effect on the germination rate (MDG) of non-aged seed produced on the primary and secondary umbels, but a delay of tertiary umbel seed germination was observed from exposure to high temperature early in seed development (Table 4-9). After accelerated aging, high temperature stress during late seed development enhanced seed germination rate especially in primary and secondary umbel seed.

Germination rate of freshly harvested barley seed was enhanced by heat stress during seed maturation stage. This enhancement was explained by the production of seeds with thinner seed coat and less inhibitor content (Khan and Laude, 1968). Laude (1967) suggested the existence during seed maturation of a sensitivity gradient to high temperature stress and reported increased germinability of heat-stressed barley seeds. More and faster germination after moderate but warm maturation temperatures was also reported for Evenari (1965), onion (Gray and Steckel, 1984), lettuce (Harrington and Thompson, 1952; Koller, 1962) and bracted plantain (Stearns, 1960).

The enhancement of seed germination percentage by warm maturation temperature was possibly due to better seed development caused by the brief high growth rate at high temperatures. It could also be attributed to thinner endosperm or lower germination inhibitors at high temperatures. Khan and Laude (1969) reported that heat stress in barley at more mature stage of seed development resulted in seeds with thinner seed coats and less inhibitor content. Von Abrams and Hand (1956) showed that normal germination in Rosa could be obtained without the need for the low temperature after-ripening treatment by exposing seed plants to high temperature and light during the 30-day period before harvest. Lexander (1980) suggested that low ripening temperature may have disturbed some seed filling reactions and high amounts of inhibitors in the seeds, while Wood et al. (1980) attributed the poor germination of sugarbeet seed developed under cooler conditions to poor seed development, thick pericarps, tight seed caps or high amounts of germination inhibitors. The possibility that only high quality seed survived the heat shock during late seed development, represent an alternative explanation to the good performance of seed which developed under normal temperature. This is supported by the reduction in seed number per umbel by brief exposure to high temperature late in seed development.

Seeds which developed under continuous high temperature produced less vigorous seedlings, with shorter hypocotyls, radicles, and lighter seed weights compared to other treatments (Table 4-10). The effect of high temperature on the progeny growth was more severe on seeds produced on primary and secondary umbels than on those developed

Table 4-10. Effect of stage of exposure to high temperatures (33/28°C) and umbel order on seedling length and seedling weight of the progenies.

Stage of exposure	Primary order	Secondary order	Tertiary order
	Radicle length (cm)		
Continuous low (20/15°C)	6.6	6.5	6.6
Continuous high (33/28°C)	1.9	3.3	5.2
Anthesis	8.5	8.4	7.2
Early seed development	8.6	8.0	6.1
Late seed development	9.0	8.8	7.3
LSD (0.05)	1.4	1.0	0.9
	Hypocotyl length (cm)		
Continuous low (20/15°C)	6.6	6.7	6.7
Continuous high (33/28°C)	4.3	5.6	5.8
Anthesis	6.6	6.9	6.6
Early seed development	6.0	6.4	6.4
Late seed development	6.7	6.1	6.0
LSD (0.05)	0.5	0.7	0.9
	Seedling fresh weight (mg)		
Continuous low (20/15°C)	25.7	23.7	25.9
Continuous high (33/28°C)	10.8	15.0	21.4
Anthesis	29.3	32.9	28.2
Early seed development	27.5	29.8	23.2
Late seed development	29.6	30.9	27.1
LSD (0.05)	5.5	3.8	3.5

Table 4-10--continued

Stage of exposure	Primary order	Secondary order	Tertiary order
	Seedling dry weight (mg)		
Continuous low (20/15°C)	0.82	0.83	0.96
Continuous high (33/28°C)	0.44	0.61	0.88
Anthesis	0.99	1.15	0.97
Early seed development	1.16	1.04	0.75
Late seed development	0.95	1.26	1.09
LSD (0.05)	0.21	0.16	0.10

on tertiary umbels. High temperature at anthesis, early or late in seed development had no effect on radicle length and seedling fresh weight. However, hypocotyl length of seedlings produced from primary umbel seed was reduced by exposure to high temperature at anthesis, while dry weight of the tertiary umbel seed progeny was reduced by exposure to high temperature at early seed development but increased by exposure to high temperature at late seed development stages (Table 4-10). High temperature early during seed development led to increased dry weight of the progeny of primary umbel seeds, while high temperature at anthesis, early or late during seed development increased dry weight of secondary umbel seed progenies (Table 4-10).

Primary umbel seeds which developed under continuous low temperature had the largest embryos followed by those which were subjected to heat shock late in their development (Table 4-11). Seeds which developed under continuous high temperature or exposed to high temperature at anthesis had the smallest embryos, followed by those subjected to high temperature early in their development. Generally, the largest embryos were obtained from seeds which were exposed to brief high temperature late in their development. Secondary umbel seeds had the largest embryos. This could be attributed to the immaturity of tertiary umbel seeds, especially those seeds which experienced low temperature late during their development.

Generally high temperature stress on progeny vigor had its greatest effect when the mother plants were maintained under high temperatures throughout seed development.

Table 4-11. Effect of stage of exposure to high temperatures (33/28°C) and umbel orders on embryo length.

Stage of exposure	Primary order	Secondary order	Tertiary order
	mm		
Continuous low (20/15°C)	1.9	1.8	1.5
Continuous high (33/28°)	1.4	1.8	1.4
Anthesis	1.5	1.5	1.4
Early seed development	1.6	1.6	1.5
Late seed development	1.8	2.0	2.1
LSD (0.05)	0.2	0.2	0.2

Summary

The effects of growing temperature on seedstalk development, seed yield and seed quality in carrots was investigated using growth chambers set at constant day/night temperatures of 33/28°C, 28/23°C, 25/20°C, 23/28°C, 20/15°C, and 17/12°C. The number of days to flowering, seedstalk height, number of umbels and seed yield decreased linearly with the increase in temperature from 17/12°C to 33/28°C.

Continuous high temperature (33/28°C) had a detrimental effect on total percentage germination with standard germination test and accelerated aging test. The optimum growing temperature to obtain optimum germination of the progeny was 20/15°C, however, faster germination was obtained when seed matured under 23/18°C temperature.

Seeds which developed at 33/28°C or 17/12°C had the smallest embryos compared to other growing temperatures. Seeds which developed at 33/28°C produced seedlings with the lowest vigor, while those which developed under 20/15°C produced seedlings with the highest vigor.

Brief exposure of carrot plants to high temperature (33/28°C) at anthesis, or early in seed development, was as detrimental to seed yield as continuous exposure to high temperature. Exposure to high temperature at late seed development had less effect on seed yield, and a positive effect on seed quality. The vigor of the progeny was greatly reduced by continuous high temperature, but unaffected by brief exposure to high temperature (33/28°C) at anthesis, early or late seed development.

The present results suggest that higher temperature during pollination, fertilization or early stages of seed development, can greatly reduce carrot seed yield and seed quality.

CHAPTER V
THE USE OF SEED PRIMING AND GROWTH REGULATORS TO ENHANCE CARROT SEED GERMINATION UNDER DIFFERENT TEMPERATURES

Introduction

Uniform field stands are a major limiting factor in the production of carrots in Florida. Carrot growers in Florida complain about exceptionally poor stands, when planting is done during the warm part of the growing season (August and September) followed by planting during the cool part of the growing season (December and January).

Seed priming has been shown to be useful in promoting seed germination under unfavorable conditions, and enhanced germination even under ideal conditions (Ells, 1963; Guedes and Cantliffe, 1977; Heydecker _et al_., 1975; Heydecker and Coolbear, 1977; Koehler, 1967; Sachs, 1977; Salter and Darby, 1976). The use of seed priming allows the seed to imbibe water slowly, thus the early stages of germination may begin, without radicle protrusion through the seed coat. Radicle protrusion may be regulated through priming under low temperature, short soak duration or by the use of solutions of low osmotic potential (Ells, 1963; Heydecker and Coolbear, 1977).

The addition of growth regulators to seeds has proved beneficial in stimulating germination under adverse conditions. Cytokinins have been used to overcome thermodormancy in lettuce seed (McCoy and

Harrington, 1970; Reynolds and Thompson, 1973). They have also been suggested as having the permissive role in seed germination, because of their ability to oppose the effect of an inhibitor and their inability to trigger seed germination (Khan, 1971).

The primary role in the control of germination can be attributed to gibberellins. The ability of gibberellins to control many germination processes has been well documented (Mayer and Shain, 1974), including the production of α-amylase by de novo synthesis in barley endosperm (Varner, 1964). Gibberellins, GA_3 and $GA_{4/7}$ have been beneficial in stimulating germination of several species under unfavorable conditions. Cotton, cucumber, lilac and pepper have all been stimulated to germinate faster and more uniformly at low temperature by GA application (Cole and Wheeler, 1974; Nelson and Sharples, 1980; Junttila, 1973; Watkins and Cantliffe, 1983).

In view of the many benefits of seed priming and growth regulators on enhancing seed germination, combining the advantages of both treatments by adding growth regulators in the priming solution might result in additional enhancement of seed germination.

Inclusion of $GA_{4/7}$ and ethephon or benzyl adenine (BA) in a PEG solution, enhanced the effects of PEG treatment on the rate of germination of celery seeds (Brocklehurst _et al_., 1982; Nakamura _et al_., 1982). Similarly, inclusion of cytokinin (kinetin or BA), $GA_{4/7}$ and ethephon in the priming solution overcame thermodormancy and enhanced lettuce seed germination at supraoptimal temperature (i.e., 35°C) (Cantliffe _et al_., 1984; Khan _et al_., 1981). So far, all the reported work on the benefits of combining priming and growth regulators, has been on seed which exhibit thermodormancy. These benefits are explainable by the role of growth regulators in circumventing thermodormancy in lettuce and celery.

The germination of carrots at low temperature was enhanced by priming (Szafirowska et al., 1981), however, the interaction between priming and seed lots was highly significant (Brocklehurst and Dearman, 1983a). Addition of growth regulators to priming solution represents one possible way to boost the germination in those lots which do not benefit greatly from priming. The experiments which follow were conducted to determine the optimum conditions for carrot seed priming and to examine the feasibility of incorporating growth regulators into priming solution to improve the performance of carrot seeds.

Materials and Methods

General Procedure

Seeds of two cultivars and three seed lots of carrots were used in the studies. Seeds of cv. Hicolor-9 were obtained from Asgrow Seed Company. Three lots of cv. Orlando Gold Hybrid were obtained from Alf Christian Seed Company, Arco Seed Company, and Petoseed Company. The performance and vigor of the last three lots are shown in Table 5-1.

Priming Solution Formulation

Polyethyleneglycol (PEG) molecular weight 8000 (Carbowax 8000), tribasic potassium phosphate (K_3PO_4) and potassium nitrate (KNO_3) were used in the first experiment to compare their effects as priming solutions. The osmotic potential of the salt solutions was calculated using Van't Hoff equation, assuming complete dissociation in solution. The formula of Michel and Kaufman (1973) was used to calculate the osmotic potential of PEG solution.

Gibberellin, GA_3 and $GA_{4/7}$, and benzylamino purine (BA) were prepared on a weight volume basis. Ethephon (Ethrel) was prepared on a volume volume basis. Gibberellin $GA_{4/7}$ was dissolved in 95% ethanol, BA in 1 N NaOH and a soluble powder of GA_3 was used. When growth regulators were applied, the final pH of the soak solution was adjusted to the original pH of PEG (6.8), which was used as a second control (PEG) besides the dry nontreated seed in all growth regulator experiments.

The Priming Technique

The standard priming procedure consisted of placing 1 g of seed in 25 x 200 mm test tubes to which 50 mL of priming solution was added. The solution was aerated through a glass tube connected to a main line by flexible plastic tubes and a hypodermic needle. The air was driven into solution by an aquarium pump. The air stream provided constant circulation of the seed within the solution. Distilled water was added daily to maintain constant volume of solution in the test tubes.

At the end of the designated soak duration, seeds were removed, rinsed with distilled water and surface moisture was removed by suction using a Buchner funnel connected to a vacuum pump. Seeds were then spread on a single layer of Whatman #3 filter paper in 9-cm petri dishes and placed to dry in the seed room at approximately 10°C and 45% R.H. Seed germination was usually evaluated within 2 weeks from the end of each experiment.

Statistical Analysis

Analysis of variance was performed on all data, using the facilities of the Northeast Regional Data Center located in Gainesville. With data expressed as percent, an arcsin transformation was used to run the analysis of variance. However, all data were presented in the original values. Mean separations between treatments were done using Duncan's Multiple Range Test.

Experiments

The following experiments were conducted during the fall and spring of 1986.

Experiment 1--The effects of priming solution, priming temperature and priming duration on the germination of carrots at 25°C. Seeds of carrot cv. Hicolor-9 were soaked in solution of KNO_3, K_3PO_4, K_3PO_4 + KNO_3 or PEG. The osmotic potential of the double salt solution was adjusted at -10 bar, while that of other solutions were adjusted at -5 or -10 bars. Seeds were soaked for 4, 7, or 14 days at 15 or 25°C. The experiment was a split plot design. Theexperiment was repeated four times, with each set representing one replication.

The number of seeds which germinated during priming were counted at the end of each duration, and based on that figure, seeds were either dried back and evaluated for germination or discarded. Standard germination tests were conducted in Petri dishes at 25°C. Total percentage germination and the MDGs were calculated on the basis of 14 days incubation.

Experiment 2--Effects of growth regulator inclusion in priming solution, priming duration and priming temperature on cv. Hicolor-9 germination. This experiment employed a basic priming solution of -10 bar PEG, based on the results of Experiment 1, to which growth regulators were added. Four priming treatments consisted of the following 1) basic solution (-10 bars PEG), 2) PEG + 100 ppm GA_3, 3) PEG + 100 ppm $GA_{4/7}$, 4) PEG + 100 BA. Priming was done at 15 or 25°C, for 7 or 14 days. Seeds were air-dried at 10°C and 45% R.H. for 14 days. The percent moisture content of the seed was 7 and 7.2% before priming and 7 days after the end of priming, respectively.

Standard germination tests were conducted at 15 and 25°C. Total percentage germination and MDGs were calculated on the basis of 14 days incubation.

Experiment 3--Response of different carrot seed lots to inclusion of growth regulator in PEG. Three seed lots of cv. Orlando Gold supplied by three seed companies, were evaluated for their response to growth regulator addition to PEG. Seeds were primed at 15°C for either 7 or 14 days. Nine priming treatments consisted of the following 1) basic solution (-10 bar PEG), 2) PEG + 100 ppm GA_3, 3) PEG + 100 ppm GA_3 + 100 ppm BA, 4) PEG + 100 ppm $GA_{4/7}$, 5) PEG + 100 ppm $GA_{4/7}$ + 100 ppm BA, 6) PEG + 100 ppm BA, 7) PEG + 500 ppm Ethrel, 8) PEG + 500 ppm Ethrel + 100 ppm GA_3, and 9) PEG + 500 ppm Ethrel + 100 ppm $GA_{4/7}$.

The experiment was designed as a split plot design. Seed lots formed the blocks, and subplots were priming treatments which formed 10 x 2 factorial in priming solutions and priming duration. Standard germination tests were conducted at 15, 25, and 35°C for 14 days. Total percentage germination and MDG were calculated at each germination temperature. Radicle length, hypocotyl length, seedling fresh weight and dry weight were measured for seed primed for 7 days and germinated at 15 and 25°C.

Results and Discussion

Experiment 1--The Effects of Priming Solution, Priming Temperature and Priming Duration on the Germination of Carrot Seeds

Radicle protrusion (pregermination) was not observed in any of the priming solution at 15 or 25°C after 4 days of priming. However, after 7 days of priming, radicle protrusion was observed, at both priming temperatures when low osmotic potential (-5 bars) solutions were used (Table 5-1). At 15°C, there was no significant difference in germination in solutions between priming solutions with low osmotic potential. Germination in solution at 25°C was higher in -5 bar PEG than -5 bar KNO_3 or K_3PO_4. Generally germination in solution at 25°C was higher than at 15°C (Table 5-1). After 14 days of priming, essentially all of the seeds germinated in -5 bar priming solution. Due to this high germination percentage, seed primed in -5 bar solutions for 7 or 14 days were excluded from the germination test.

Table 5-1. The effects of priming solution and priming temperature on seed germination in the priming solution after 7 days.

Priming solution	Priming temperature (°C) 15	25
	Germination (%)	
- 5 bars PEG	13 a[x]	62 a[x]
-10 bars PEG	0 b	0 c
- 5 bars KNO_3	7 a	23 b
-10 bars KNO_3	0 b	0 c
- 5 bars K_3PO_4	12 a	24 b
-10 bars KNO_3 + K_3PO_4	0 b	0 c

[x] Means within a column separated by LSD, p = 5%.

The results of this experiment indicated that carrot seed can be primed safely for 4 days at -5 bar solutions, however, for longer priming durations, the osmotic potential of the priming solution should be low enough to completely inhibit radicle protrusion. Prevention of radicle protrusion should be considered as a major criterion for evaluating priming solutions if seed redrying after priming is intended.

Averaged over priming duration and priming solution, priming temperature had no effect on germination percentage (Table 5-2). Priming for 4, 7 or 14 days at 25°C, when averaged over priming solutions, had no effect on percent germination.

Priming in the double salt solution for 4 days at 15°C resulted in lower percent germination when compared to nontreated seeds while soaking in other solutions for 4 days had no effect on percent germination (Table 5-2). Total percentage germination was unaffected by 7 days priming in any solution at 15°C, but when priming was done for 7 days at 25°C, salt solutions with high osmotic potential (-10 bar) significantly reduced percent germination. Such an adverse effect on germination was not observed with the use of -10 bar PEG solution (Table 5-2).

The use of high osmotic potential solution of KNO_3 for priming at 15 or 25°C, or the double salts at 25°C reduced total germination when soaking duration was extended to 14 days. Priming at 25°C resulted in faster germination, compared to priming at 15°C, when averaged over priming duration and priming solution (Table 5-3). Priming for 7 or 14 days at 15°C resulted in faster germination, compared to 4 days

Table 5-2. The effects of priming temperature, priming solution and priming duration on total percentage germination at 25°C of carrot seed cv. Hicolor-9.

Priming temp.	Priming solution	Priming duration (days) 4	7	14
15°C	Control	74 a[x]	66 a	72 ab
	− 5 bars PEG	70 ab	–	–
	−10 bars PEG	74 a	68 a	79 a
	− 5 bars KNO_3	77 a	–	–
	−10 bars KNO_3	64 ab	57 a	55 c
	− 5 bars K_3PO_4	66 ab	–	–
	−10 bars K_3PO_4	64 ab	68 a	66 bc
	−10 bars KNO_3 + K_3PO_4	60 b	61 a	68 ab
Priming duration mean		69 a[y]	62 b	68 ab
Temperature mean			67 a[y]	
25°C	Control	75 a	76 a	79 a
	− 5 bars PEG	67 a	–	–
	−10 bars PEG	70 a	77 a	80 a
	− 5 bars KNO_3	69 a	–	–
	−10 bars KNO_3	70 a	49 b	37 b
	− 5 bars K_3PO_4	64 a	–	–
	−10 bars K_3PO_4	67 a	59 b	67 a
	−10 bars KNO_3 + K_3PO_4	64 a	56 b	36 b
Priming duration mean		68 a[y]	63 a	60 a
Temperature mean			65 a	

[x] Means within columns separated by LSD, p = 5%.

[y] Means within rows separated by LSD, p = 5%.

Table 5-3. The effects of priming temperature, priming solution and priming duration on mean days to germination (MDG) at 25°C of carrot seed cv. Hicolor-9.

Priming temp.	Priming solution	Priming duration (days)		
		4	7	14
15°C	Control	3.2 a	3.4 a	3.1 a
	- 5 bars PEG	2.5 cd	-	-
	-10 bars PEG	2.7 bc	2.2 bc	1.8 c
	- 5 bars KNO_3	2.2 d	-	-
	-10 bars KNO_3	2.3 cd	1.8 b	1.8 c
	- 5 bars K_3PO_4	2.2 d	-	-
	-10 bars K_3PO_4	2.8 b	2.0 b	2.4 b
	-10 bars KNO_3 + K_3PO_4	3.3 a	1.9 b	2.2 b
Priming duration mean		2.7 a	2.2 b	2.3 b
Temperature mean			2.4 b	
25°C	Control	3.2 a	3.2 a	3.0 a
	- 5 bars PEG	2.8 ab	-	-
	-10 bars PEG	2.5 b	2.4 bc	2.1 b
	- 5 bars KNO_3	2.4 b	-	-
	-10 bars KNO_3	1.8 c	2.5 bc	1.9 b
	- 5 bars K_3PO_4	3.2 a	-	-
	-10 bars K_3PO_4	2.5 b	2.9 ab	2.1 b
	-10 bars KNO_3 + K_3PO_4	2.6 b	2.3 c	3.0 a
Priming duration mean		2.6 a	2.6 a	2.4 a
Temperature mean			2.6 a	

[x] Means within columns separated by LSD, p = 5%.

[y] Means within rows separated by LSD, p = 5%.

duration. However, at 25°C priming temperature, priming duration had no effect on MDG.

Priming in the double salt solution for 4 days at 15°C had no effect on MDG, while all other priming solutions reduced MDG at 25°C when compared to nontreated seeds. When priming was done at 25°C for 4 days, -5 bar PEG and K_3PO_4 did not affect MDG, however, other priming solutions advanced germination at 25°C.

At 15°C priming temperature, soaking in all solutions for 7 or 14 days reduced the MDG compared to the control, with no differences between priming solutions within each duration. At 25°C, priming temperature, soaking in -10 bar K_3PO_4 for 7 days or the double salt solution for 14 days had no effect on MDG at 25°C (Table 5-3).

The results of this experiment indicated that the composition of the priming solution is as important as the osmotic potential of the solution. The osmoticum of the priming solution must control water uptake by the seed, but some salt solutions especially KNO_3 and NaCl at high concentrations, can be toxic to seed. Poor germination was reported when NaCl was used as soak solution for tomato, alfalfa, and lettuce (Mayer and Poljakoff-Mayber, 1975) and $CaCl_2$ for peas (Heydecker, 1967). Reduction of the final percentage germination in many vegetable seeds (unspecified species) and tomato when KNO_3 was used as priming solution was reported by Aker and Brede (1986) and Odell (1986). The advantages of PEG as priming agent arise from its make-up of larger molecules, which cannot enter the cell, allowing water only to enter the seed (Heydecker, 1973). Ions from a salt solution can enter the cell with water without slowing water uptake

(Cantliffe et al., 1984) and by doing so, cell damage can occur at higher concentrations of salt, especially if priming continues for longer duration.

Experiment 2—Effects of Growth Regulators Inclusion in Priming Solution, Priming Duration and Priming Temperature on cv. Hicolor-9 Germination

Germination at 15°C

Priming at 15°C resulted in higher percent germination, compared to priming at 25°C, when averaged over duration and solution (Table 5-4). However, this difference in percent germination between 15 and 25°C was of no practical significance.

Total percentage germination at 15°C was not improved by any priming treatment at both prime temperatures. On the contrary, less germination was obtained with 14 days priming in PEG + GA_3 and PEG + $GA_{4/7}$ at 15°C, 4 days priming in PEG + GA_3 and PEG + BA at 15°C and 4 days priming in PEG + $GA_{4/7}$ at 25°C (Table 5-4). Comparison between soak durations, within treatments, indicated that extending the duration from 7 to 14 days had no effect on total percent germinatin.

Priming in PEG + $GA_{4/7}$ for 4 days at 15 and 25°C and 7 or 14 days at 15°C had no effect on the mean days to germination. However, all other priming solutions, at both prime temperatures, resulted in faster germination, compared to the control (Table 5-5).

Table 5-4. The effects of soak temperature, soak duration and incorporation of growth regulators in polyethylene glycol (PEG) on total percentage germination of cv. Hicolor-9 at 15°C.

Priming temp.	Priming solution	Priming duration (days)			
		4	7	14	Mean
15°C	Control	84 ab[x] a[y]	78 a a	78 a a	80 ab
	PEG	86 a a	79 a a	83 a a	83 a
	PEG + GA$_3$ (100 ppm)	71 c ab	78 a a	62 b b	70 c
	PEG + GA$_{4/7}$ (100 ppm)	75 bc a	78 a a	65 b a	73 c
	PEG + BA (100 ppm)	72 c a	75 a a	79 a a	75 c
Soak duration mean		78 a[y]	78 a	73 a	
Temperature mean			76 a		
25°C	Control	78 a a	78 a a	77 a a	78 a
	PEG	72 ab a	76 a a	78 a a	75 a
	PEG + GA$_3$ (100 ppm)	77 a a	76 a a	78 a a	77 a
	PEG + GA$_{4/7}$ (100 ppm)	63 b a	66 a a	68 a a	66 b
	PEG + BA (100 ppm)	76 a a	70 a a	68 a a	71 ab
Soak duration mean		73 a[y]	73 a	74 a	
Temperature mean			73 b		

[x] Means within columns separated by LSD, p = 5%.

[y] Means within rows separated by LSD, p = 5%.

Table 5-5. The effects of soak temperature, soak duration and incorporation of growth regulators in polyethylene glycol (PEG) on mean days to germination of cv. Hicolor-9 at 15°C.

Priming temp.	Priming solution	Priming duration (days)			
		4	7	14	Mean
15°C	Control	5.4 a[x] a[y]	5.5 a a	5.6 a a	5.5 a
	PEG	4.1 b a	3.7 bc ab	3.3 b b	3.7 b
	PEG + GA_3 (100 ppm)	4.1 b a	3.3 c b	3.6 b ab	3.7 b
	PEG + $GA_{4/7}$ (100 ppm)	5.5 a a	5.3 a a	5.9 a a	5.6 a
	PEG + BA (100 ppm)	3.9 b a	3.9 b a	3.3 b a	3.7 a
Soak duration mean		4.6 a	4.3 a	4.3 a	
Temperature mean			4.4 a		
25°C	Control	5.6 a a	5.1 a a	5.2 a a	5.3 a
	PEG	4.1 b a	3.6 c a	3.1 b a	3.6 c
	PEG + GA_3 (100 ppm)	4.3 b a	3.4 c a	3.0 b a	3.6 c
	PEG + $GA_{4/7}$ (100 ppm)	6.0 a a	3.9 bc b	3.1 b b	4.3 b
	PEG + BA (100 ppm)	4.5 b a	4.3 b a	2.9 b b	3.9 c
Soak duration mean		4.9 a	4.1 b	3.4 c	
Temperature mean			4.1 b		

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[x] Means within columns separated by LSD, p = 5%.

[y] Means within rows separated by LSD, p = 5%.

Germination at 25°C

Total percentage germination was unaffected by 4 or 7 days priming in all solutions, at both prime temperatures. After 14 days priming, reduction in percent germination was observed with the use of PEG + BA at both temperatures (Table 5-6).

Compared to a nontreated control, priming for 14 days resulted in faster germination, regardless of the treatment. Mean days to germination was unaffected by priming in PEG + $GA_{4/7}$ for 4 days at both prime temperatures and 7 days at 15°C (Table 5-7).

It could be concluded that total percent germination of Hicolor-9 at 15 and 25°C was not improved by priming treatment, however, faster germination at both temperatures was achieved by all priming treatments, with the exception of PEG + $GA_{4/7}$, at all prime temperatures and durations.

Experiment 3—The Response of Different Carrot Seed Lots of the Cv. Orlando Gold to Incorporation of Growth Regulators in PEG

The performance and vigor of the three lots used in this experiment are shown in Table 5-8. Total percent germination at 15°C of lot 1 was increased with 7 days priming in PEG, PEG + BA or PEG + Ethrel + GA_3 and 14 days priming in PEG alone (Table 5-9). The increase in soak duration to 14 days reduced percent germination, when averaged over soak solutions, compared to 7 days duration. However, when durations were compared within each solution, no effect was observed.

Table 5-6. The effects of soak temperature, soak duration and incorporation of growth regulators in PEG on total percentage germination of cv. Hicolor-9 at 25°C.

Priming temp.	Priming solution	Priming duration (days)			
		4	7	14	Mean
15°C	Control	73 a^{x} a^{y}	73 a a	74 ab a	73 ab
	PEG	80 a a	77 a a	81 a a	80 a
	PEG + GA_3 (100 ppm)	77 a a	76 a a	67 abc a	73 ab
	PEG + $GA_{4/7}$ (100 ppm)	80 a a	69 a a	63 bc a	71 b
	PEG + BA (100 ppm)	78 a a	75 a a	56 c b	70 b
Soak duration mean		78 a^{y}	74 ab	68 b	
Temperature mean			73 a		
25°C	Control	74 a a	70 a a	67 b a	70 a
	PEG	74 a a	71 a a	83 a a	76 a
	PEG + GA_3 (100 ppm)	69 a a	76 a a	81 a a	75 a
	PEG + $GA_{4/7}$ (100 ppm)	74 a ab	65 a b	80 a a	73 a
	PEG + BA (100 ppm)	73 a a	69 a a	63 b a	68 a
Soak duration mean		73 a^{y}	70 a	75 a	
Temperature mean			73 a		

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[x] Means within columns separated by LSD, p = 5%.

[y] Means within rows separated by LSD, p = 5%.

Table 5-7. The effects of soak temperature, soak duration and incorporation of growth regulators in PEG on mean days to germination (MDG) of cv. Hicolor-9 at 25°C.

Priming temp.	Priming solution	Priming duration (days)			Mean
		4	7	14	
15°C	Control	3.0 a a^{y}	2.8 a a	2.9 a a	2.9 a
	PEG	2.4 b a	1.8 b b	1.4 c b	1.9 c
	PEG + GA_3 (100 ppm)	2.4 b a	1.6 b b	1.7 c b	1.9 c
	PEG + $GA_{4/7}$ (100 ppm)	2.9 a a	2.7 a a	2.4 b a	2.7 b
	PEG + BA (100 ppm)	2.3 b a	1.8 b ab	1.7 c b	1.9 c
Soak duration mean		2.6 a	2.1 b	2.0 b	
Temperature mean			2.2 a		
25°C	Control	2.9 a a	2.8 a a	2.8 a a	2.8 a
	PEG	2.2 c a	2.0 c ab	1.5 cd b	1.9 c
	PEG + GA_3 (100 ppm)	2.1 c a	1.7 d ab	1.5 d b	1.8 c
	PEG + $GA_{4/7}$ (100 ppm)	2.8 ab a	2.2 b ab	1.8 bc b	2.3 b
	PEG + BA (100 ppm)	2.5 b a	2.4 b a	1.7 b b	2.2 b
Soak duration mean		2.5 a	2.2 a	1.9 a	
Temperature mean			2.2 a		

[x] Means within columns separated by LSD, p = 5%.

[y] Means within rows separated by LSD, p = 5%.

Table 5-8. The germination of three seed lots of Orlando Gold at 15, 25 and 35°C after 0, 2 and 4 days of aging at 41°C and 100% relative humidity.

Aging	Seed lot	Germination temperature (°C)		
		15	25	35
days		Germination percentage (%)		
0	1	94	68	3
	2	89	56	0
	3	86	61	5
2	1	58	55	0
	2	49	45	0
	3	18	18	0
4	1	23	6	0
	2	7	12	0
	3	0	2	0
		Mean days to germination (days)		
0	1	5.3	4.8	4.3
	2	6.4	7.5	-
	3	6.4	6.1	11.5
2	1	7.8	5.5	-
	2	9.7	7.2	-
	3	11.0	7.4	-
4	1	11.1	9.5	-
	2	10.7	9.8	-
	3	-	9.0	-

Table 5-9. The effects of seed lot, growth regulators incorporation into PEG and soak duration on total percentage germination of carrot seed cv. Orlando Gold at 15°c.

Soak duration (days)	Seed lot #1		Duration signif.	Seed lot #2		Duration signif.	Seed lot #3		Soak duration significance	Means
	7	14		7	14		7	14		
	%									
Soak solution										
Control	81 c[x]	75 b	NS	83 a	88 a	NS	77 a	80 ab	NS	81 c
PEG	94 ab	93 a	NS	91 a	93 a	NS	82 a	88 a	NS	90 a
PEG + GA_3 (100 ppm)	85 bc	78 b	NS	91 a	81 a	NS	82 a	69 bc	*	81 c
PEG + GA_3 + BA	81 c	75 b	NS	93 a	89 a	NS	76 a	61 c	*	79 c
PEG + $GA_{4/7}$ (100 ppm)	83 bc	86 ab	NS	91 a	90 a	NS	77 a	80 ab	NS	85 bc
PEG + $GA_{4/7}$ + BA	84 bc	73 b	NS	83 a	82 a	*	66 a	70 bc	NS	78 c
PEG + BA (100 ppm)	95 a	84 ab	NS	92 a	87 a	NS	66 a	70 bc	NS	82 bc
PEG + Ethrel (500 ppm)	84 bc	88 ab	NS	88 a	85 a	NS	73 a	78 ab	NS	83 bc
PEG + Ethrel + GA_3	91 ab	80 b	NS	95 a	89 a	NS	79 a	84 ab	NS	86 b
PEG + Ethrel + $GA_{4/7}$	83 bc	76 b	NS	90 a	82 a	NS	76 a	80 ab	NS	81 c
Soak duration mean	86 a[y]	81 b		91 a	87 b		75 a	76 a		
Seed lot mean			83 b			89 a			76 c	

[x] Means within columns separated by LSD, p = 5%.

[y] Means within rows separated by LSD, p = 5%.

Total percent germination at 15°C of lot 2 was unaffected by priming for 7 or 14 days in any of the solutions (Table 5-9). Similar to lot 1, longer soak duration reduced percent germination, when averaged over all treatments. When compared within treatment, priming in PEG + $GA_{4/7}$ + BA for 14 days caused a reduction in percent germination when compared to 7 days priming in the same solution.

Priming solutions had no effect on percent germination at 15°C of lot 3, when priming was done for 7 days. However, priming in PEG + GA_3 + BA for 14 days reduced percent germination, when compared to the nontreated control or basic PEG solution (Table 5-9). A similar reduction in germination was caused with the addition of GA_3, $GA_{4/7}$ + BA or BA to PEG, when compared to PEG alone. Averaged over all priming solutions, 14 days duration had no effect on germination, compared to 7 days duration, but priming in PEG + GA_3 or PEG + GA_3 + BA for 14 days reduced percent germination, when compared to 7 days priming in the same solutions.

Averaged over priming solutions, percent germination at 15°C of lots 1 and 2 were lower after 14 days of priming than 7 days, while that of lot 3 was unaffected by prime duration. Averaged over priming solutions, and priming duration, percent germination at 15°C of lot 2 was higher than that of lot 1, which in turn, was higher than that of lot 3 (Table 5-9).

At 15°C, MDG of lot 1 was unaffected by 7 days priming in any priming solution (Table 5-10). Fourteen days priming in PEG, PEG + GA_3 or PEG + BA reduced MDG, when compared to nontreated or priming in PEG + $GA_{4/7}$ for 14 days. Longer duration of priming in PEG, PEG +

GA_3, PEG + GA_3 + BA or PEG + BA, reduced MDG compared to shorter duration.

The addition of GA_3, $GA_{4/7}$, Ethrel, Ethrel + GA_3 or Ethrel + $GA_{4/7}$ to PEG reduced MDG, at 15°C of lot 2, after 7 days priming, compared to the nontreated control. However, none of these solutions resulted in advancement in germination rate, when compared to PEG alone (Table 5-10). Fourteen days priming in PEG, PEG + $GA_{4/7}$ or PEG + Ethrel + $GA_{4/7}$ had no effect on MDG at 15°C. The only reduction in MDG, compared to PEG, was obtained with addition of 100 ppm BA.

When lot 3 seeds were primed for 7 days, MDG at 15°C was reduced only by PEG + GA_3. After 14 days of priming, PEG or PEG with either GA_3 + BA, BA, Ethrel, Ethrel + GA_3 or Ethrel + $GA_{4/7}$ improved germination rate at 15°C. Priming for 7 days resulted in faster germination, compared to 14 days, with PEG + GA_3, and slower germination with PEG + Ethrel + $GA_{4/7}$.

Averaged over priming solutions, germination at 15°C of lot 1 and 2 was faster after 14 days of priming than 7 days, while that of lot 3 was unaffected by soak duration. When averaged over soak solutions and soak duration, lot 2 has slower germination at 15°C, compared to lots 1 and 3, which were similar (Table 5-10).

At 25°C, percent germination of lot 1 was reduced by priming in PEG + GA_3 + BA for 7 or 14 days, and unaffected by other priming treatments (Table 5-11). Percent germination of lot 2 was unaffected by priming in PEG + GA_3, or PEG + $GA_{4/7}$ + BA for 7 days and increased by the remaining priming treatments. When soak duration was increased to 14 days, percent germination at 25°C of lot 2 was increased by the

Table 5-10. The effects of seed lot, growth regulators incorporation into PEG and soak duration on mean days to germination of carrot seed cv. Orlando Gold at 15°C.

Soak duration (days)	Seed lot #1		Duration	Seed lot #2		Duration	Seed lot #3		Soak duration	
	7	14	signif.	7	14	signif.	7	14	significance	Means
	days									
Soak solution										
Control	5.8 abc	5.4 ab	NS	7.5 a	6.9 a	NS	5.8 a	6.3 a	NS	6.3 a
PEG	5.4 abc	4.0 cd	*	6.8 ab	6.3 ab	NS	4.8 ab	4.5 cd	NS	5.3 c
PEG + GA_3 (100 ppm)	5.2 abc	4.1 cd	*	6.2 bc	5.3 bc	*	4.2 b	5.8 ab	*	5.1 c
PEG + GA_3 + BA	5.9 ab	4.4 bcd	*	7.0 ab	5.6 bc	*	4.7 ab	4.2 d	NS	5.3 c
PEG + $GA_{4/7}$ (100 ppm)	6.0 ab	5.3 ab	NS	6.2 bc	5.7 abc	NS	5.6 a	5.4 abc	NS	5.7 b
PEG + $GA_{4/7}$ + BA	6.1 a	5.2 abc	NS	6.3 abc	5.8 abc	NS	5.6 a	5.4 abc	NS	5.7 b
PEG + BA (100 ppm)	5.7 abc	3.9 d	*	7.2 ab	4.8 c	*	5.5 a	5.0 bcd	NS	5.3 c
PEG + Ethrel (500 ppm)	4.6 c	4.1 bcd	NS	5.5 cd	5.6 bc	NS	5.5 a	5.0 bcd	NS	5.0 c
PEG + Ethrel + GA_3	4.9 bc	4.4 bcd	NS	5.0 d	5.5 bc	NS	5.2 ab	5.0 bcd	NS	5.0 c
PEG + Ethrel + $GA_{4/7}$	4.9 bc	5.8 a	NS	6.2 bc	6.4 ab	NS	5.8 a	4.8 bcd	*	5.6 b
Soak duration mean	5.5 a[y]	4.6 b		6.4 a	5.8 b		5.3 a	5.1 a		
Seed lot mean			5.1 b			6.1 a			5.2 b	

[x] Means within columns separated by LSD, p = 5%.

[y] Means within rows separated by LSD, p = 5%.

addition of Ethrel + GA_3 or Ethrel + $GA_{4/7}$ to the PEG solution, compared to the nontreated control. Germination of lot 3 was increased by priming in PEG for 7 days, or PEG + Ethrel + GA_3 and PEG + Ethrel for 14 days.

In all three seed lots, the addition of growth regulators to PEG did not result in any additional benefit in total germination at 25°C when compared to PEG alone. An increase in prime duration from 7 to 14 days had no effect on percent germination in all three lots, when averaged over all priming treatments. When priming durations were compared within treatments at the 25°C germination temperature, 14 days priming resulted in lower percent germination in lot 1 and higher percent germination in lot 3, when priming was done in PEG + Ethrel + GA_3 and lower percent germination in lot 3 when seeds were primed in PEG + GA_3.

Priming in PEG + Ethrel + $GA_{4/7}$ for 7 days decreased germination rate (MDG) at 25°C of lot 1, however there was no effect of the other treatments, when compared to nontreated control (Table 5-12). After 14 days of priming, PEG, PEG + GA_3, PEG + BA and PEG + Ethrel + GA_3 significantly increased germination rate.

At 25°C, all priming treatments at both durations reduced MDG of lot 2. The only advantage of increasing priming duration to 14 days was observed with priming in PEG + GA_3, PEG + $GA_{4/7}$ or PEG + BA (Table 5-12). Germination rate of lot 3 at 25°C was increased by priming in PEG, PEG + GA_3, PEG + BA or PEG + Ethrel + GA_3 for 7 days. However, after 14 days of priming, PEG + $GA_{4/7}$ was the only treatment which did not reduce MDG of lot 3.

Table 5-11. The effects of seed lot, growth regulators incorporation into PEG and soak duration on total percentage germination of carrot seed cv. Orlando Gold at 25°c.

	Seed lot #1		Duration	Seed lot #2		Duration	Seed lot #3		Soak duration	
Soak duration (days)	7	14	signif.	7	14	signif.	7	14	significance	Means
					%					
Soak solution										
Control	86 a[x]	84 ab	NS	66 b	73 b	NS	60 b	55 cd	NS	71 cd
PEG	82 a	90 a	NS	78 a	86 ab	NS	81 a	69 abcd	NS	81 a
PEG + GA_3 (100 ppm)	88 a	81 ab	NS	82 a	71 b	NS	67 b	52 d	*	73 bc
PEG + GA_3 + BA	55 b	45 c	NS	86 a	82 ab	NS	57 b	66 bcd	NS	65 d
PEG + $GA_{4/7}$ (100 ppm)	80 a	79 ab	NS	85 a	87 ab	NS	67 ab	75 abc	NS	79 ab
PEG + $GA_{4/7}$ + BA	76 a	68 b	NS	81 a	71 b	NS	60 b	58 cd	NS	69 cd
PEG + BA (100 ppm)	84 a	79 ab	NS	86 a	85 ab	NS	67 ab	66 bcd	NS	78 ab
PEG + Ethrel (500 ppm)	79 a	80 ab	NS	89 a	78 ab	NS	68 ab	81 ab	NS	79 ab
PEG + Ethrel + GA_3	85 a	71 b	*	85 a	89 a	NS	61 ab	83 a	*	79 ab
PEG + Ethrel + $GA_{4/7}$	71 ab	76 ab	NS	89 a	92 a	NS	65 ab	72 abcd	NS	78 ab
Soak duration mean	78 a[y]	75 a		82 a	8a 1		65 a	68 a		
Seed lot mean			77 a[y]			82 a			67 a	

[x] Means within columns separated by LSD, p = 5%.

[y] Means within rows separated by LSD, p = 5%.

Table 5-12. The effects of seed lot, growth regulators incorporation into PEG and soak duration on mean days to germination of carrot seed cv. Orlando Gold at 25°C.

Soak duration (days)	Seed lot #1		Duration signif.	Seed lot #2		Duration signif.	Seed lot #3		Soak duration significance	Means
	7	14		7	14		7	14		
	days									
Soak solution										
Control	4.6 bc[x]	4.4 a	NS	6.5 a	6.1 a	NS	5.2 a	5.3 a	NS	5.3 a
PEG	3.8 bc	2.9 bc	NS	4.7 b	3.6 b	NS	3.5 cd	3.6 bcd	NS	3.7 cd
PEG + GA_3 (100 ppm)	4.4 bc	2.8 c	*	4.3 b	3.5 b	*	3.2 d	2.8 d	NS	3.5 d
PEG + GA_3 + BA	4.9 ab	3.5 abc	*	4.8 b	4.2 b	NS	4.1 abcd	4.1 bc	NS	4.3 b
PEG + $GA_{4/7}$ (100 ppm)	4.7 bc	4.0 abc	NS	4.8 b	3.8 b	*	4.6 abc	4.3 ab	NS	4.3 b
PEG + $GA_{4/7}$ + BA	4.5 bc	3.9 abc	NS	4.5 b	4.2 b	NS	4.4 abcd	4.2 bc	NS	4.3 b
PEG + BA (100 ppm)	4.8 bc	3.0 bc	*	5.0 b	3.8 b	*	3.9 bcd	3.3 bcd	*	3.9 c
PEG + Ethrel (500 ppm)	3.5 c	3.2 abc	NS	3.9 b	3.7 b	NS	4.9 ab	3.3 bcd	*	3.7 cd
PEG + Ethrel + GA_3	3.9 bc	2.9 bc	NS	4.1 b	3.5 b	NS	3.8 bcd	3.0 cd	*	3.6 d
PEG + Ethrel + $GA_{4/7}$	6.0 a	4.2 ab	*	4.3 b	3.7 b	NS	4.4 abcd	4.1 bc	NS	4.4 b
Soak duration mean	4.5 a[y]	3.5 b		4.7 a	4.0 b		4.2 a	3.8 b		
Seed lot mean			4.0 b			4.3 a			4.0 b	

[x] Means within columns separated by LSD, p = 5%.

[y] Means within rows separated by LSD, p = 5%.

Averaged over all priming solutions, MDG at 25°C of all three lots was reduced by 14 days of priming compared to 7 days. Generally, addition of growth regulators to PEG showed no additive benefit with respect to germination rate (MDG) at 25°C of all three lots, compared to priming in PEG alone.

Only small percentage of the seeds of all three lots germinated at 35°C unless the carrot seeds were primed. Percentage germination at 35°C of lot 1 was increased by 7 days priming in PEG, PEG + BA or PEG + Ethrel and 14 days priming in PEG or PEG + Ethrel (Table 5-13). However, none of the treatments that increased germination were significantly different from using PEG alone. Regardless of prime duration, the highest percentage germination was obtained with the use of PEG alone.

All priming treatments at both durations significantly increased percentage germination at 35°C of lot 2 compared to the nontreated control. Similar to lot 1, germination at 35°C was not improved by addition of growth regulators to PEG. Priming for 7 days in PEG, PEG + Ethrel or PEG + Ethrel + $GA_{4/7}$ significantly increased percentage germination at 35°C of lot 3. When prime duration was extended to 14 days, PEG + GA_3 + BA, PEG + $GA_{4/7}$ + BA and PEG + BA were the only treatments that did not improve percentage germination.

In all three lots, the effectiveness of PEG in increasing percent germination at 35°C was not additionally increased by addition of any growth regulators. Priming in PEG or PEG + Ethrel were the only treatments which significantly increased percentage germination at 35°C, in all three lots at both prime durations. Averaged over all

Table 5-13. The effects of seed lot, growth regulations incorporation and soak duration on total percentage germination of carrot seed cv. Orlando Gold at 35°C.

Soak duration (days)	Seed lot #1 7	Seed lot #1 14	Duration signif.	Seed lot #2 7	Seed lot #2 14	Duration signif.	Seed lot #3 7	Seed lot #3 14	Soak duration significance	Means
	%									
Soak solution										
Control	14 cd[x]	9 cd	NS	10 b	7 b	NS	19 cd	7 c	NS	11 f
PEG	76 a	85 a	NS	53 a	76 a	*	77 a	75 a	NS	74 a
PEG + GA_3 (100 ppm)	50 abcd	32 bcde	*	54 a	81 a	*	51 abc	52 ab	NS	53 bc
PEG + GA_3 + BA	13 d	8 de	NS	57 a	69 a	NS	8 d	21 bc	*	29 e
PEG + $GA_{4/7}$ (100 ppm)	36 abcd	53 abc	*	50 a	79 a	*	53 abd	60 ab	NS	55 bc
PEG + $GA_{4/7}$ + BA	29 bcd	13 cde	*	65 a	75 a	NS	27 bcd	31 bc	NS	40 d
PEG + BA	62 ab	46 bc	NS	82 a	76 a	NS	17 cd	21 bc	NS	51 c
PEG + Ethrel (500 ppm)	67 ab	68 ab	NS	64 a	81 a	NS	61 ab	75 a	NS	69 a
PEG + Ethrel + GA_3	54 abc	42 bcd	NS	62 a	80 a	NS	53 abc	60 ab	NS	59 b
PEG + Ethrel + $GA_{4/7}$	44 abcd	43 bcd	NS	64 a	77 a	NS	60 ab	58 ab	NS	58 b
Soak duration mean	45 a[y]	40 a		56 b	70 a		43 a	46 a		
Seed lot mean			42 b[y]			63 a			44 b	

[x] Means within columns separated by LSD, p = 5%.

[y] Means within rows separated by LSD, p = 5%.

treatments within seed lots, priming for 14 days increased percentage germination of lot 2, but had no effect on that of lots 1 and 3. Averaged over all treatments and soak duration, seed lot 2 had a higher percentage germination at 35°C compared to lots 1 and 3.

Soaking in PEG + GA_3 or PEG + Ethrel + GA_3 for 7 days and in PEG, PEG + GA_3, PEG + GA_3 + BA, or PEG + Ethrel + GA_3 for 14 days significantly increased germination rate of lot 1 at 35°C (Table 5-14). With 7 days priming, germination rate of lot 2 was unaffected by PEG + $GA_{4/7}$, and increased by all other treatments compared to the nontreated control. After 14 days priming, only PEG + GA_3 and PEG + GA_3 + BA increased germination rate of lot 2 at 35°C. Priming in PEG for 7 days or priming in general for 14 days, increased germination rate of lot 3 at 35°C germination temperature (Table 5-14).

When averaged over all treatments within each lot, 14 days duration was superior to 7 days duration in reducing time to germination in all three lots. Averaged over priming durations and priming solutions, seed lot 3 had the most rapid germination rate followed by lots 1 and 2.

The three seed lots used in experiment 3 belong to the cv. Orlando Gold, which is the major cultivar grown in Florida. They were produced in the same year by three different seed companies. Seed lot 2 had the highest germination percentage at all germination temperatures, i.e., 15, 25 and 35°C. There was no clear difference between lots 1 and 3. The effect of priming treatments was dependent on the seed lot. At 15°C germination temperature, total germination percent was not affected by priming in all three lots. This is due to

Table 5-14. The effects of seed lot, growth regulators incorporation and soak duration on mean days to germination of carrot seed cv. Orlando Gold at 35°C.

	Seed lot #1		Duration	Seed lot #2		Duration	Seed lot #3		Soak duration	
Soak duration (days)	7	14	signif.	7	14	signif.	7	14	significance	Means
	days									
Soak solution										
Control	6.9 a[x]	6.3 a	NS	8.7 a	7.9 a	NS	7.2 ab	8.2 a	NS	7.3 a
PEG	5.6 ab	3.9 b	*	6.2 bc	4.9 ab	NS	3.9 c	2.8 b	NS	4.5 de
PEG + GA$_3$ (100 ppm)	5.0 b	3.8 b	NS	5.8 c	3.9 b	NS	4.4 bc	3.1 b	NS	4.3 e
PEG + GA$_3$ + BA	6.1 ab	4.1 b	*	7.1 bc	3.9 b	*	5.0 bc	2.4 b	*	4.7 de
PEG + GA$_{4/7}$ (100 ppm)	5.6 ab	5.0 ab	NS	7.6 ab	4.8 ab	*	6.2 abc	4.5 b	NS	5.6 c
PEG + GA$_{4/7}$ + BA	6.2 ab	6.2 a	NS	7.1 bc	5.3 ab	NS	8.5 a	5.0 b	*	6.4 b
PEG + BA (100 ppm)	6.1 ab	5.1 ab	NS	6.5 bc	4.9 ab	NS	5.1 bc	2.7 b	*	5.1 cd
PEG + Ethrel (500 ppm)	5.5 ab	4.6 ab	NS	6.0 bc	4.3 ab	NS	5.6 bc	4.4 b	*	5.1 cd
PEG + Ethrel + GA$_3$	4.7 b	3.9 b	NS	6.1 bc	4.4 ab	NS	4.9 bc	3.4 b	NS	4.6 de
PEG + Ethrel + GA$_{4/7}$	5.7 ab	5.3 ab	NS	6.2 bc	5.1 ab	NS	7.0 ab	4.5 b	*	5.6 c
Soak duration mean	5.7 a[y]	4.8 b		6.7 a	4.7 b		5.8 a	4.1 b		
Seed lot mean			5.3 ab[y]			5.7 a			4.9 b	

[x] Means within columns separated by LSD, p = 5%.

[y] Means within rows separated by LSD, p = 5%.

the high germination of the nontreated seed. However, the increase in germination rate at 15°C was greatly affected by seed lot quality. After 7 days of priming, the germination rate of lot 1 was not improved by any priming treatment, that of lot 3 increased by one treatment, while that of lot 2 was increased by five of the nine treatments.

The germination rate and total germination of lot 2 at 25 and 35°C were increased by almost all priming treatments at both prime durations. Total germination percent of lot 1 at 25°C was unaffected by priming treatment and that at 35°C was increased by three of the nine treatments. The germination rate of lot 1 was increased by only four treatments and that increase was obtained after 14 days of priming. The germination rate of lot 3 at 25 and 35°C was increased by all treatments, when priming was done for 14 days. However, the germination percent at 25°C was increased by only three treatments.

Thus, greater response to seed priming in carrot, can be obtained with the use of seed lots of high initial quality. For seed lots with low or intermediate quality, longer prime duration could help in improving the response of seedlots to priming, but cannot overcome the effect of the initial seed quality. Seed lots 1 and 3 contained higher amounts of green (immature) seed compared to lot 2, which could explain their low response to priming. Perkins-Veazie and Cantliffe (1984) reported that only lettuce seeds of the highest quality could be effectively primed to overcome thermodormancy. Higher germination rate after priming carrot seed was obtained with seed lots which initially had the fastest germination (Brocklehurst and Dearman, 1983a).

Germination of all seed lots at high temperature (35°C) was consistently increased by priming for 7 or 14 days in PEG alone or PEG + Ethrel, with no difference between PEG and PEG + Ethrel. Germination of lettuce (Heydecker et al., 1975; Guedes and Cantliffe, 1977) and celery (Salter and Darby, 1976) was increased at supraoptimal temperature by seed priming. The increase in carrot seed germination at high temperature by seed priming suggests the removal of biochemical and/or morphological block(s) to germination at high temperature by seed priming. Guedes et al. (1981) reported that seed priming appeared to loosen the lettuce endosperm, which might relate to promotion of germination at 35°C. Also priming seed at a low temperature may be leaching some growth inhibitors that prevent germination (Khan et al., 1978).

Germination of all seed lots was lower at 35°C, intermediate at 25°C and higher at 15°C. This explains the poor stand of carrots during early planting (August and September) in Florida. Thus, the use of primed seed during early planting is highly recommended, since, germination percent at 35°C of all three lots was significantly increased by seed priming.

The germination rate (MDG) of all seed lots at all germination temperatures was not improved by addition of growth regulators to PEG, compared to PEG alone. However, in all cases in which seed lots showed no response to PEG, the effectiveness of PEG in increasing germination rate was increased by adding growth regulators, namely

GA_3, Ethrel or their combination. Based on that, addition of GA_3, Ethrel or GA_3 + Ethrel during priming of low quality seed lots could be safely recommended.

A recent study by Tucker and Gray (1986) demonstrated that $GA_{4/7}$ soak improved germination of immature carrot seeds, but had no effect on the germination of mature seeds. Austin et al. (1969) suggested that hydration of carrot seeds may allow the embryo of some seeds to "after-ripen," which may be chemical or morphological or possibly membrane modification.

The development of immature carrot seed can continue provided that they are held above 30% moisture content. In the present study, moisture content of the seed was above 30% after 24 hours of priming and by the end of priming, it was above 50%. Thus, it is possible that the effect of priming on seed germination is the result of embryo growth, caused by the higher water content of the seed during priming. Storage of moist Heracleum seed at low temperature (Stokes, 1952) and hardening of carrot seed (Austin et al., 1969) resulted in embryo growth by increasing cell division.

The lack of response to the addition of growth regulators to PEG, when compared to PEG, could be attributed to high level of endogenous growth promoters, the de novo synthesis of growth promoters during priming or leaching of germination inhibitors during the priming process.

Seedling Growth

Seedling growth in all three lots was measured at 15 anad 25°C. Due to the poor germination and seedling growth at 35°C, the data for that temperature are not presented. The effects of priming treatments on seedling growth was evaluated using seed primed for 7 days.

Seedling growth at 15°C

Seedling hypocotyl length, radicle length and fresh weight at 15 and 25°C of all lots were reduced by addition of BA at 100 ppm to PEG. Combining GA_3 or $GA_{4/7}$ with BA did not overcome BA effect on radicle length, hypocotyl length and fresh weight (Table 5-15). Seedling dry weight was not affected by BA incorporation in PEG in all three lots.

Seedling radicle length of lot 1 was increased by priming in PEG, PEG + GA_3, PEG + $GA_{4/7}$ and PEG + Ethrel + $GA_{4/7}$ at 15°C. Addition of GA_3 to PEG had no effect on radicle length of lot 2 at 15°C.. All other treatments that had no BA increased radicle length. When germinated at 15°C, radicle length of lot 3 was reduced by all BA-containing solutions, unaffected by addition of GA_3, Ethrel or Ethrel + GA_3 to PEG and increased by PEG, PEG + $GA_{4/7}$ and PEG + Ethrel + $GA_{4/7}$ (Table 5-15).

At 15°C, hypocotyl length of seedlings from lot 1 was reduced by all priming treatments, that of lot 2 was reduced by addition of either GA_3, Ethrel + $GA_{4/7}$, BA or BA in combination with GA_3 or $GA_{4/7}$ to PEG, and unaffected by the remaining treatments. Incorporation of GA_3, $GA_{4/7}$ or Ethrel in PEG, had no effect on hypocotyl length of lot 3 seedlings at 15°C, while priming in PEG increased and priming in solution containing BA reduced hypocotyl length (Table 5-15).

Table 5-15. The effects of incorporation of growth regulators into PEG on seedling growth of three seed lots of cv. Orlando Gold at 15°C.

Treatment	Lot #1	Lot #2	Lot #3
		Radicle length (cm)	
Control	5.2 d^x	2.2 c	3.9 cd
PEG	7.3 ab	2.8 ab	5.0 a
PEG + GA$_3$ (100 ppm)	7.9 a	2.4 bc	4.2 cd
PEG + GA$_3$ + BA	2.2 e	0.8 f	0.9 e
PEG + GA$_{4/7}$ (100 ppm)	7.4 ab	3.1 a	4.7 ab
PEG + GA$_{4/7}$ + BA	3.0 e	1.3 d	1.2 e
PEG + BA (100 ppm)	2.5 e	1.1 de	0.7 e
PEG + Ethrel (500 ppm)	6.1 c	2.7 ab	4.3 bc
PEG + Ethrel + GA$_3$	5.8 cd	3.0 a	3.6 d
PEG + Ethrel + GA$_{4/7}$	6.7 bc	0.6 f	4.9 ab
		Hypocotyl length (cm)	
Control	7.5 a	3.7 a	4.7 b
PEG	6.6 b	3.8 a	5.2 a
PEG + GA$_3$ (100 ppm)	6.5 b	2.9 b	4.6 b
PEG + GA$_3$ + BA	2.6 d	1.3 cd	0.9 e
PEG + GA$_{4/7}$ (100 ppm)	6.0 bc	4.1 a	4.2 bc
PEG + GA$_{4/7}$ + BA	2.1 d	1.4 c	1.1 e
PEG + BA (100 ppm)	2.3 d	1.6 c	1.0 e
PEG + Ethrel (500 ppm)	5.6 c	3.8 a	4.3 b
PEG + Ethrel + GA$_3$	5.3 c	3.7 a	3.5 d
PEG + Ethrel + GA$_{4/7}$	6.0 bc	0.9 d	3.7 cd
		Fresh weight (mg)	
Control	28.3 a	8.5 bc	13.3 ab
PEG	25.3 bc	10.3 a	14.0 a
PEG + GA$_3$ (100 ppm)	20.0 a	8.3 c	13.8 a
PEG + GA$_3$ + BA	22.0 de	6.0 d	8.3 cd
PEG + GA$_{4/7}$ (100 ppm)	22.5 cde	9.5 ab	13.0 ab
PEG + GA$_{4/7}$ + BA	19.8 e	6.5 d	7.0 d
PEG + BA (100 ppm)	20.5 e	6.3 d	9.0 c
PEG + Ethrel (500 ppm)	24.3 bcd	9.5 ab	14.3 a
PEG + Ethrel +GA$_3$	22.5 cde	8.0 c	11.8 b
PEG + Ethrel + GA$_{4/7}$	22.5 cde	6.0 d	12.5 ab

Table 5-15--continued.

Treatment	Lot #1	Lot #2	Lot #3
		Dry weight (mg)	
Control	1.13 a	0.40 a	0.68 ab
PEG	1.07 ab	0.38 ab	0.73 a
PEG + GA_3 (100 ppm)	1.13 a	0.35 ab	0.48 c
PEG + GA_3 + BA	1.05 a	0.25 b	0.55 bc
PEG + $GA_{4/7}$ (100 ppm)	1.05 a	0.35 ab	0.60 ab
PEG + $GA_{4/7}$ + BA	0.98 bc	0.38 ab	0.63 ab
PEG + BA (100 ppm)	1.10 ab	0.40 a	0.70 a
PEG + Ethrel (500 ppm)	1.05 ab	0.40 a	0.68 ab
PEG + Ethrel + GA_3	0.88 c	0.40 a	0.60 ab
PEG + Ethrel + $GA_{4/7}$	0.98 bc	0.43 a	0.63 ab

[x] Means within columns separated by LSD, p = 5%.

At 15°C germination temperature, fresh weight of lot 2 was increased by PEG and reduced by PEG + Ethrel + $GA_{4/7}$ or addition of BA to PEG, that of lot 1 unaffected by PEG + GA_3 and reduced by all other treatments, while fresh weight of lot 3 was reduced only when BA was added to PEG (Table 5-15).

Seedling dry weight of lot 1 at 15°C was reduced by PEG + Ethrel + GA_3, PEG + Ethrel + $GA_{4/7}$ and PEG + $GA_{4/7}$ + BA, that of lot 2 by PEG + GA_3 + BA, while that of lot 3 was only reduced by incorporation of GA_3 into PEG solution (Table 5-15).

Seedling growth at 25°C

Radicle length, hypocotyl length and fresh weight of all 3 lots were reduced by the addition of BA at 100 ppm to PEG. Combining GA_3 or $GA_{4/7}$ with BA had no effect on the inhibitory effects of BA on seedling growth (Table 5-16).

At 25°C, seedling radicle length of lot 1 was increased by priming in PEG, PEG + GA_3 and PEG + $GA_{4/7}$. That of lot 2 was increased by all priming treatments, which did not contain BA. Addition of Ethrel + GA_3 to PEG had no effect on radicle length of lot 3, however, all other treatments with no BA significantly increased radicle length.

Seedling hypocotyl length of lot 1 was reduced by the addition of Ethrel + $GA_{4/7}$ to PEG. Other treatments, except BA-containing treatments had no effect on the hypocotyl length of all 3 lots (Table 5-16). The inhibition of seedling radicle and hypocotyl growth by BA was reported on lettuce (Seale, 1986) and tomato (Odell, 1986).

Table 5-16. The effects of growth regulators incorporated into Polyethyleneglycol (PEG) on seedling growth of three seed lots of cv. Orlando Gold at 25°C.

Treatment	Lot #1	Lot #2	Lot #3
		Radicle length (cm)	
Control	5.8 c^x	2.5 d	4.3 d
PEG	7.4 ab	3.3 c	5.4 ab
PEG + GA_3 (100 ppm)	8.4 a	4.2 ab	5.9 ab
PEG + GA_3 + BA	2.2 d	1.2 e	1.0 e
PEG + $GA_{4/7}$ (100 ppm)	7.9 a	3.9 bc	6.2 a
PEG + $GA_{4/7}$ + BA	2.9 d	1.1 e	1.6 e
PEG + BA (100 ppm)	1.9 d	1.0 e	0.8 e
PEG + Ethrel (500 ppm)	5.5 c	3.7 bc	5.2 bc
PEG + Ethrel + GA_3	6.3 bc	4.6 a	4.5 cd
PEG + Ethrel + $GA_{4/7}$	5.2 c	4.3 ab	5.2 bc
		Hypocotyl length (cm)	
Control	7.4 a	5.1 ab	6.2 a
PEG	6.9 ab	5.2 ab	6.2 a
PEG + GA_3 (100 ppm)	7.1 ab	5.8 a	5.6 b
PEG + GA_3 + BA	2.0 g	2.5 cd	1.7 c
PEG + $GA_{4/7}$ (100 ppm)	6.6 bc	5.2 a	6.1 ab
PEG + $GA_{4/7}$ + BA	2.7 f	2.7 c	1.9 c
PEG + BA (100 ppm)	2.7 f	1.8 d	1.5 c
PEG + Ethrel (500 ppm)	5.8 de	5.4 ab	5.7 ab
PEG + Ethrel + GA_3	6.1 cd	5.1 ab	5.9 ab
PEG + Ethrel +$GA_{4/7}$	5.2 e	4.9 b	5.9 ab
		Fresh weight (mg)	
Control	28.5 ab	10.5 c	16.0 a
PEG	30.8 a	12.3 ab	17.3 a
PEG + GA_3 (100 ppm)	27.5 ab	13.8 a	17.0 a
PEG + GA_3 + BA	18.0 e	8.8 e	10.8 b
PEG + $GA_{4/7}$ (100 ppm)	25.8 bc	11.3 bc	16.3 a
PEG + $GA_{4/7}$ + BA	22.8 cd	8.8 d	9.5 b
PEG + BA (100 ppm)	20.5 d	7.5 d	10.3 b
PEG + Ethrel (500 ppm)	26.6 abc	12.5 ab	16.0 a
PEG + Ethrel + GA_3	26.0 bc	13.3 a	16.8 a
PEG + Ethrel + $GA_{4/7}$	22.5 cd	11.0 bc	17.8 a

Table 5-16--continued.

Treatment	Lot #1	Lot #2	Lot #3
		Dry weight (mg)	
Control	0.95 bc	0.32 bcd	0.50 b
PEG	1.07 ab	0.35 abc	0.53 b
PEG + GA_3 (100 ppm)	1.18 a	0.40 ab	0.58 ab
PEG + GA_3 + BA	0.95 bc	0.30 cd	0.55 ab
PEG + $GA_{4/7}$ (100 ppm)	0.90 bc	0.30 cd	0.65 a
PEG + $GA_{4/7}$ + BA	0.90 bc	0.25 d	0.53 b
PEG + BA (100 ppm)	0.88 bc	0.25 d	0.48 b
PEG + Ethrel (500 ppm)	0.93 bc	0.40 ab	0.50 b
PEG + Ethrel + GA_3	0.90 bc	0.40 ab	0.58 ab
PEG + Ethrel + $GA_{4/7}$	0.78 c	0.43 a	0.53 b

[x] Means within columns separated by LSD, p = 5%.

Planting of BA-treated seed in the field would result in poor stand of carrot, due to the slow rate of radicle elongation caused by BA, and the possibility of food reserve depletion before the exposure of photosynthetic tissues to light. Thus, evaluation of growth regulators effect on seedling growth, in addition to seed germination, appeared to be of great importance, before recommending such treatment for use.

The increase in radicle length by priming treatments could be attributable to the earlier germination of primed seeds compared to the nontreated seed. Radicle length in carrots always correlates with root size and crop yield. An increase in radicle length would probably result in longer root and higher crop yield. Based on that assumption, higher yield in all three lots could be expected by priming in PEG, PEG + GA_3 or PEG + $GA_{4/7}$.

Gibberellin was reported to cause an extra elongation of the hypocotyl of many species of seedlings. Such phenomenon is called spindly seedling (Heydecker and Coolbear, 1977). Such undesirable effect of gibberellin was not observed in all seed lots, when GA_3 or $GA_{4/7}$ was added to PEG.

Seedling fresh weight of all three lots at 25°C, was reduced by the addition of BA to PEG. In addition, fresh weight of lot 1 was reduced by PEG + Ethrel + $GA_{4/7}$ (Table 5-16). Seedling dry weight of lots 1, 2, and 3 increased by PEG + GA_3, PEG + Ethrel and PEG + $GA_{4/7}$, respectively. All other priming treatments had no effect on seedling dry weight.

Summary

A series of experiments were conducted to investigate the effects of prime osmoticum, temperature, duration and seed lot variability to addition of growth regulators to prime osmoticum.

In the first experiment, PEG, KNO_3, and K_3PO_4 at -5 and -10 bar and KNO_3 + K_3PO_4 at -10 bar were tested as osmotic media for priming carrot seeds cv. Hicolor-9 at 15 or 25°C for 4, 7, and 14 days. Soaking seeds in -5 bar solution of PEG, KNO_3 or K_3PO_4 at 15 or 25°C resulted in higher germination of seed in the priming solution, after 7 days of soaking. Increasing the osmotic potential to -10 bar completely prevented seed germination in the priming solutions at both priming temperatures. Germination rate of carrot seed was increased by all osmotic solutions, but higher germination percentage was consistently obtained with the use of -10 bar PEG as prime solution.

In the second experiment, either GA_3, $GA_{4/7}$ or BA at 100 ppm each were added to PEG to compare their effect on the germination of Hicolor-9 seeds. Priming was performed at 15 or 25°C for 4, 7 or 14 days. Total percent germination at 15 and 25°C was unaffected by priming treatments, however, the germination rate was increased by PEG, PEG + GA_3 and PEG + BA at all prime temperatures and durations.

In experiment 3, three seed lots of cv. Orlando Gold, produced in the same year by three seed companies, were used to study seed lot variability to addition of growth regulators to osmotic solution. Gibberellin, GA_3 or $GA_{4/7}$ at 100 ppm, alone or combined with 100 ppm BA or 500 ppm Ethrel, BA or Ethrel were incroporated in -10 bar PEG solution to form nine treatments. Seed were primed for 7 or 14 days

at 15°C and seed germination was evaluated at 15, 25 and 35°C. The effect of seed priming in PEG on total germination in all three lots was not improved by the addition of growth regulators. Seed priming was more effective in improving seed performance at 25°C than 15°C, and was highly effective at high temperature (35°C). The effect of priming treatment was dependent on seed lot quality. Germination at 25 and 35°C of lot 2, which had the highest quality, was improved by all treatments regardless of prime duration, while that of lots 1 and 3 was only improved after 14 days of priming by some of the treatments.

The use of high quality seed for priming is recommended to obtain the best results from priming. The use of primed seed during the warm part of the growing season in Florida, could result in an improved carrot stand. Although addition of GA_3, Ethrel or GA_3 + Ethrel to PEG did not result in improvement in seed performance, compared to PEG, their addition helped improve the germination, compared to the nontreated control, whenever PEG failed to do so. Thus, addition of GA_3, GA_3 + Ethrel or Ethrel might improve the performance of some seed lots which do not respond to priming in PEG alone.

CHAPTER VI
SUMMARY

A greenhouse experiment, a growth chamber experiment and a series of laboratory experiments were conducted to investigate the influence of seedstalk development, seed production temperature and priming treatments on the germination of carrot seeds.

The main objective of the greenhouse experiment was to investigate the possibility of using growth regulators to modify seedstalk development in carrot seed plants and to determine the effect of such modification on seed yield and seed quality. Seedstalk height was increased by application of GA_3 at 1000 ppm and reduced by Ancymidol, Daminozide, CCC and Phosphon-D. Ancymidol at 25 to 250 ppm, Daminozide at 1000 to 5000 ppm and hand pruning reduced the total number of branches per plant and total seed yield. The amount of seed produced by primary and secondary umbels was increased while that produced by tertiary and quaternary umbels was decreased by Ancymidol, Daminozide and hand pruning. When growth regulators were applied during the summer, they were ineffective in reducing total number of branches, compared to their application during the fall. Such lack of effectiveness was attributed to the effect of high temperature during the summer on level of GA in the plants.

Both chemical and hand pruning did not result in improvement of seed quality. Tertiary umbel seeds, which were reduced by pruning, had the highest germination and produced the most vigorous seedlings, compared to seeds from primary and secondary umbels, which were increased by pruning. Under field conditions, delaying carrot seed harvest to allow tertiary umbel seeds to reach maturity is recommended for improving carrot seed quality.

The influence of growing temperature on seedstalk development, seed yield and seed quality in carrot was investigated using growth chambers set at constant day/night temperatures of 33/28°C, 28/23°C, 25/20°C, 23/18°C, 20/15°C, and 17/12°C. The number of days to flowering, seedstalk height, total number of umbels per plant and seed yield decreased linearly with the increase in temperature from 17/12°C to 33/28°C.

Continuous high temperature (33/28°C) had a detrimental effect on seed germination. The optimum seed production temperature to obtain optimum germination of the progeny was 20/15°C, however, faster germination was obtained when seed matured under 23/18°C temperature.

Brief exposure (10 days) of carrot plants to high temperature (33/28°C) at anthesis or during early seed development was as detrimental to seed yield and seed quality as continuous exposure to high temperature. Brief exposure to high temperature at late seed development had less effect on seed yield and significantly improved seed quality.

Germination rate of carrot seeds at 15 and 25°C was increased by soaking seeds for 14 days in -10 bar KNO_3, K_3PO_4 or PEG solutions. However, higher germination percentage was consistently obtained with the use of -10 bar PEG as the soak solution.

Three seed lots of cv. Orlando Gold, produced in the same year by three seed companies, were used to study seed lot variability to addition of growth regulator to PEG. The effectiveness of PEG in improving performance of all three lots was not increased by the addition of growth regulators. Seed priming was more effective in improving seed performance at 25°C than at 15°C. At 35°C, seeds of all three lots failed to germinate without priming. The response of seed lot to priming treatments was greatly affected by the initial seed quality. Germination of seed lot with initial high quality was improved by all priming treatments, while those with initial low quality were improved by fewer treatments.

The use of high quality seed for priming could result in further improvement in seed performance by priming. Planting primed seed especially during the warm part of the growing season in Florida, is highly recommended for establishing good stands of carrots.

APPENDIX
DATA TABLES FOR CHAPTERS III AND IV

Table A-1. Planting and harvest dates for Experiments I, II, and III.

Experiment	Season	Seed sowing (field)	Root harvest (field)	Root planting (greenhouse)	Seed harvest (greenhouse)
I	Fall 1983	Apr. 14	Aug. 9	Nov. 14	Mar. 15
II	Summer 1984	Sept. 27	Feb. 15	Mar. 30	July 11
III	Fall 1984	Apr. 19	Aug. 22	Nov. 3	Mar. 17

Table A-2. Average weekly temperature in the greenhouse during fall 1983 and summer 1984.

Date	Maximum (°C)	Minimum (°C)
10/24/83	29	13
10/31/83	28	14
11/7/83	26	13
11/14/83	31	12
11/21/83	33	14
11/28/83	27	16
12/5/83	25	13
12/12/83	22	12
12/29/83	19	11
1/2/84	22	11
1/9/84	18	12
1/16/84	27	13
1/23/84	31	15
1/30/84	38	16
2/6/84	38	16
2/13/84	34	17
2/20/84	29	18
2/27/84	29	17
3/7/84	32	19
3/14/84	32	19
3/21/84	30	19
3/28/84	32	17
4/9/84	37	14
4/16/84	37	14
4/23/84	37	18
4/30/84	41	17
5/7/84	43	17
5/14/84	44	18
5/21/84	42	21
5/28/84	40	17
6/2/84	43	21
6/9/84	43	22
6/17/84	42	24
6/24/84	42	23
7/2/84	46	22
7/9/84	44	24
7/16/84	42	23
7/23/84	43	22
7/30/84	45	24
8/13/84	44	24
8/20/84	42	22
8/20/84	42	22
8/27/84	46	22
9/3/84	38	21

Table A-2--continued.

Date	Maximum (°C)	Minimum (°C)
11/1/84	33	17
11/8/84	34	16
11/15/84	31	18
11/22/84	35	18
11/29/84	36	21
12/6/84	30	17
12/13/84	31	13
12/20/84	34	15
12/27/84	29	16
1/4/85	29	13
1/11/85	32	12
1/18/85	29	13
1/25/85	32	13
2/1/85	32	14
2/8/85	27	12
2/15/85	31	13
2/22/85	31	12
2/29/85	35	16
3/7/85	35	13
3/14/85	33	16
3/21/85	34	14

Table A-3. Effects of chemical regulators on number of days to primary umbel anthesis, seedstalk height, number of umbels per order and total number of umbels per plant, Experiment II, summer 1984.

Treatment	No. days to 1st anthesis	Seedstalk height	Number of umbels per order			Total no. umbels per plant
			2°	3°	4°	
— ppm —		— cm —				
Control	83	57	7	19	15	42
Ancymidol 100	62	36	7	17	10	35
Ancymidol 250	67	26	4	13	10	28
Daminozide 2000	75	32	7	17	16	41
Daminozide 5000	67	36	8	16	12	37
Chlormequat 2000	74	39	6	16	17	40
Chlormequat 5000	65	28	6	13	16	55
Phosphon-D 250	81	34	7	30	17	55
Phosphon-D 500	66	32	11	20	7	39
Contrast						
Control vs. Other	NS[z]	**	NS	NS	NS	NS
Ancymidol vs. Daminozide	NS	NS	NS	NS	NS	NS
Ancymidol 100 vs. 250	NS	NS	NS	NS	NS	NS
Daminozide 2000 vs. 5000	NS	NS	NS	NS	NS	NS
Chlormequat vs. Phosphon-D	NS	NS	*	**	NS	NS
Chlormequat 2000 vs. 5000	NS	NS	NS	NS	NS	NS
Phosphon-D 250 vs. 500	NS	NS	NS	*	NS	NS

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[z] F values significant at 0.01 level (**), 0.05 level (*), or not significant (NS).

Table A-4. Effects of chemical regulators on seed yield of each umbel order and total seed yield per plant, Experiment II, summer, 1983.

Treatment	Umbel order 1°	Umbel order 2°	Umbel order 3°	Umbel order 4°	Total seed yield
— ppm —	gm seed/umbel order				— gm seed/plant —
Control	3.3	5.3	3.2	0.3	12.1
Ancymidol 100	2.0	4.0	4.2	0.5	10.7
Ancymidol 250	1.8	3.5	3.6	0.5	9.4
Daminozide 2000	1.2	2.5	1.8	0.2	5.6
Daminozide 5000	2.0	4.4	3.3	0.4	10.1
Chlormequat 2000	2.7	4.4	2.9	1.4	11.3
Chlormequat 5000	2.1	4.1	3.4	0.1	9.8
Phosphon-D 250	2.2	4.0	3.3	0.7	10.1
Phosphon-D 500	1.2	2.2	1.4	0.3	4.8
Contrast					
Control vs. Other	*[z]	*	NS	NS	NS
Ancymidol vs. Daminozide	NS	NS	NS	NS	NS
Ancymidol 100 vs. 250	NS	NS	NS	NS	NS
Daminozide 2000 vs. 5000	NS	NS	NS	NS	NS
Chlormequat vs. Phosphon-D	NS	NS	NS	NS	NS
Chlormequat 2000 vs. 5000	NS	NS	NS	*	NS
Phosphon-D 250 vs. 500	NS	NS	NS	NS	*

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[z] F values significant at 0.01 level (**), 0.05 level (*), or not significant (NS).

Table A-5. Effects of various chemical regulators on the contribution (%) of different umbel orders to the final seed yield for Experiment II, summer 1984.

Treatment	Umbel order					
	1°	2°	1° and 2°	3°	4°	3° and 4°
— ppm —	% seed per umbel order					
Control	29.4	43.3	72.5	26.0	2.9	28.9
Ancymidol 100	19.4	36.9	56.3	32.5	11.1	43.6
Ancymidol 250	21.0	38.0	59.1	37.1	3.8	40.9
Daminozide 2000	24.6	49.2	73.8	23.3	2.9	26.2
Daminozide 5000	18.6	45.1	63.7	31.9	4.4	36.3
Chlormequat 2000	26.2	43.3	69.5	19.7	10.8	20.5
Chlormequat 5000	23.0	42.8	65.9	32.6	1.5	34.1
Phosphon-D 250	26.6	40.3	66.9	28.4	4.8	33.1
Phosphon-D 500	25.2	55.6	80.9	17.8	0.0	17.8
Contrast						
Control vs. Other	NS[z]	NS	NS	NS	NS	NS
Ancymidol vs. Daminozide	NS	NS	NS	NS	NS	NS
Ancymidol 100 vs. 250	NS	NS	NS	NS	*	NS
Daminozide 2000 vs. 5000	NS	NS	NS	NS	NS	NS
Chlormequat vs. Phosphon-D	NS	NS	NS	NS	NS	NS
Chlormequat 2000 vs. 5000	NS	NS	NS	NS	NS	NS
Phosphon-D 250 vs. 500	NS	NS	NS	NS	NS	NS

[z] F values significant at 0.01 level (**), 0.05 level (*), or not significant (NS).

Table A-6. Effects of chemical regulators and seed aging on total percentage germination and mean days to germination for Experiment II, summer 1984.

Treatment	Aging		Aging	
	-	+	-	+
— ppm —	— % germination —		Mean days to germination	
Control	96[z]	51	2.9[y]	7.3
Ancymidol 100	81	45	2.8	6.1
Ancymidol 250	73	29	5.8	9.8
Daminozide 2000	82	42	4.2	7.1
Daminozide 5000	82	29	3.8	7.0
Chlormequat 2000	92	77	3.1	5.7
Chlormequat 5000	93	82	3.9	5.6
Phosphon-D 250	94	86	3.1	5.2
Phosphon-D 500	96	68	3.3	5.5

[z] LSD (0.05) for treatment x aging = 13%.

[y] LSD (0.05) for treatment x aging = 0.6 day.

Table A-7. Daily maximum and minimum temperature (°C) at Jefferson County, Oregon State, during carrot seed production season, 1986.

Date	May		June	
	Max	Min	Max	Min
1	18	-2	38	17
2	19	2	36	16
3	14	3	32	14
4	13	-1	32	13
5	14	1	27	9
6	9	0	27	5
7	13	-1	22	6
8	16	-1	19	3
9	16	1	23	4
10	13	-2	28	8
11	11	-2	33	12
12	13	-2	34	11
13	19	2	33	10
14	17	-3	34	14
15	18	-1	23	6
16	19	0	26	8
17	23	2	22	7
18	28	6	25	9
19	23	7	18	3
20	26	8	23	4
21	16	3	22	6
22	14	-2	26	9
23	18	1	32	12
24	21	7	36	13
25	30	11	33	12
26	33	13	33	11
27	31	11	32	12
28	30	11	33	17
29	32	13	31	11
30	36	16	24	6
31	38	17		

July		August		September	
Max	Min	Max	Min	Max	Min
29	13	32	10	27	7
32	13	34	15	27	9
22	10	33	13	29	11
23	7	33	9	32	11
16	3	32	7	32	11
22	5	32	9	31	10
28	9	33	12	23	7
29	11	34	13	28	6
29	11	37	15	19	7
24	12	38	15	19	6
23	11	32	9	21	2
27	7	28	8	22	2
26	6	29	9	19	4
29	8	32	12	19	1
23	4	37	12	18	2
19	6	33	11	17	2
18	4	32	11	16	2
26	6	34	12	14	4
28	9	35	9	16	3
32	12	31	10	17	7
33	12	31	12	16	8
34	8	33	11	18	3
29	8	31	12	22	3
29	8	29	9	14	7
31	9	29	11	12	4
29	8	32	12	13	3
25	6	34	14	11	3
27	7	29	16	14	2
28	8	30	13	13	3
27	7	27	11	15	3
27	8	22	7		

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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